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A TEXTBOOK OF GENERAL BOTANY

By

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FROM THE PREFACE TO THE FIRST EDITION

This book is an outgrowth of the experience of the authors in the teaching of elementary botany at the University of Wisconsin. For the past three years the text, in successively revised form, has been used in our first-year courses.

In its preparation, we have been guided by the view that the subject of botany should be presented as a unit. The beginning student is not interested in, and should not be burdened with, distinctions between the artificially abstracted phases of the subject—morphology, physiology, ecology, and the like—distinctions which have their place in defining and limiting the scope of more advanced and special courses. Especially should the study of structure and that of function be intimately correlated in an elementary course.

It is hardly necessary, in the present state of development of the teaching of science, to point out that forms selected for study should, whenever possible, be such as are already known to the student, either because of their widespread occurrence in nature or in cultivation, or because of their economic importance; or that general conceptions should be illustrated by familiar facts. Particularly—in botany—should the beginning of the study be an observation of everyday plants. Considerations such as these have guided us in the choice of material to be used in an elementary course.

In a subject the teaching of which involves the introduction of the student to many new concepts, the use of a new terminology is unavoidable. However, the authors realize that each new term imposes an additional burden upon the student and correspondingly handicaps him in the mastery of the subject matter. We have attempted, therefore, to avoid technical terms except those which were found indispensable to a clear presentation.

Only such facts and conceptions have been introduced as our experience has shown can be successfully treated in the course of the beginning year. Necessarily the subject matter has been arranged in what seems to the authors a logical order, on the assumption of a continuous year's course. However, in many

institutions, conditions necessitate the offering of a briefer elementary course in botany. We have tried to provide for the possibility of such a course by so treating various topics that, within reasonable limits, certain chapters and portions of chapters may be omitted without destroying the continuity of the course or impairing the utility of the later parts of the book.

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A TEXTBOOK OF GENERAL BOTANY

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CHAPTER I

THE MAKE-UP OF A PLANT

1. A Plant and Its Parts. It is helpful to begin the study of plants by a consideration of one which is familiar, and at the same time large and easily handled. Such a plant is the sunflower (Fig. 1). The sunflower is not only a member of the group of most complex plants (the *seed plants*); it is also one of the most highly developed members of that group. One noticeable characteristic of the sunflower plant is that it is made up of distinct parts. These parts of which the plant is composed are called *organs*. The organs that are present at almost any stage in the development of the plant are *leaves*, *stem*, and *roots*. Certain other organs may or may not be present; occasionally, for example (especially in certain varieties of the sunflower), *branches*, which, as will appear, can conveniently be classed with the stem; and *flowers* and *fruits*—organs whose study may better be left until later.

In order to remain alive, to grow, and to reproduce—that is, to give rise to new plants—the sunflower plant must do certain work. The different kinds of work that a plant carries on are spoken of as its *functions*. In order to understand a plant, it is necessary to learn as much as possible about its *structure*—that is, about the parts of which it is composed, their form and arrangement; and also about its functions—the work that it does. It is always true that, in a general way, a plant is so constituted as to be able to perform its functions successfully; and so the structure of a plant can not be understood without a familiarity with its functions, nor can its functions be understood without a knowledge of its structure.

What has just been said of a plant as a whole applies also to its separate organs. The work of a plant is in large measure

divided between the organs of which it is composed. Each organ is so constituted that it is fitted to carry on a certain function or certain functions better than other organs of the plant can perform them. There is a considerable degree of division of labor between the organs, each doing especially the work for which its structure best fits it. It becomes necessary, therefore, to study each separate organ likewise from the standpoints of structure and of function.

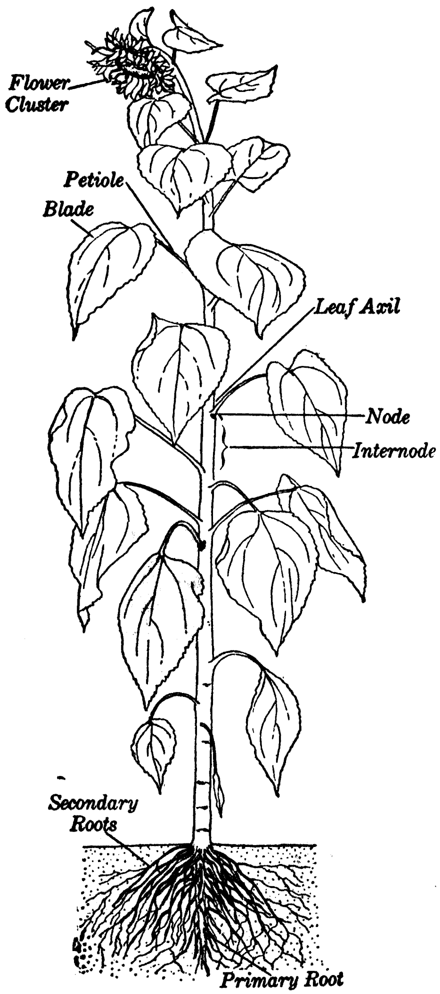


FIG. 1. A sunflower plant.

2. Leaf of the Sunflower. A leaf of the sunflower (Fig. 2) is made up of two parts: a slender stalk, or *petiole*, and a broad *blade*. A leaf blade held between the eye and the light is seen to be marked by many light green lines which are called *veins*. There is one large central vein (*midrib*), from both sides of which run smaller branch veins; these branch veins send off finer branches, these in turn still finer ones, and so on; the smallest branches run together here and there, so that the whole blade is penetrated by a close network of veins large and small. The positions of the larger veins are marked by ridges on the under surface of the blade. The parts of the leaf—petiole, blade, and veins—have, to some extent, different functions; that is, just as there is a division of labor between the organs that

make up the plant, so there is a division of labor between the parts of a single organ such as a leaf. Similarly, a stem or a root is made up of different parts, each doing its share of the work of the organ as a whole.

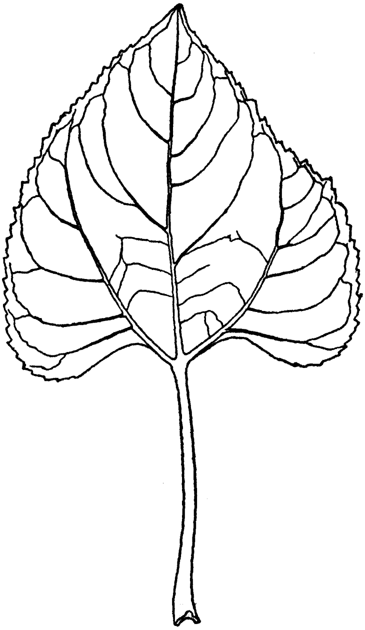


FIG. 2. Leaf of a sunflower, showing the arrangement of veins.

3. Other Types of Leaves. Although the more familiar and larger plants are in general composed of the same organs as is the sunflower, these organs differ greatly in form in different plants. A leaf of the Indian corn (Fig. 3) is long and slender, and is divided, not into blade and petiole as is the sunflower leaf, but into blade and *sheath.* The sheath, or basal part of the leaf, is a clasping structure which surrounds the stem for some distance above the level at which the leaf is really attached. There is a difference also in the arrangement of the veins. Whereas the conspicuous veins of the sunflower leaf are much branched and form a network, those of the corn leaf run approximately parallel from the base to the apex of the blade. The appearance of the vein systems in the two cases is very different; in reality both leaves have branch veins, but the branch veins in the corn leaf are very fine and not easily seen.

4. Stems and Branches. Both sunflower and corn (Fig. 4) have upright stems each consisting of *nodes,* or joints, at which the leaves are borne, and *internodes* (the portions of each stem between successive nodes). The stem of the corn is commonly thought of as unbranched; there are, however, occasional branches (suckers) which grow from near its base. The tassels and ears, which bear flowers, are also branches, or systems of branches. An important characteristic of the sunflower plant is in the fact that older parts of the stem or branches gradually increase in thickness as long as the plant is growing. The method of growth

by which this *secondary thickening* takes place will be described in Chapter V. The corn stem, on the other hand, has no such means of secondary thickening.

5. Roots. The original (*primary*) root of a sunflower plant is a direct continuation of the stem. Sooner or later this primary root produces lateral branches (*secondary roots*) which may themselves branch. Production of secondary roots results in a rather widespread *root system* in which the branches are, for the most part, progressively smaller, the ultimate branches being very slender. The roots of the sunflower have a method of secondary thickening similar to that of stems and branches.

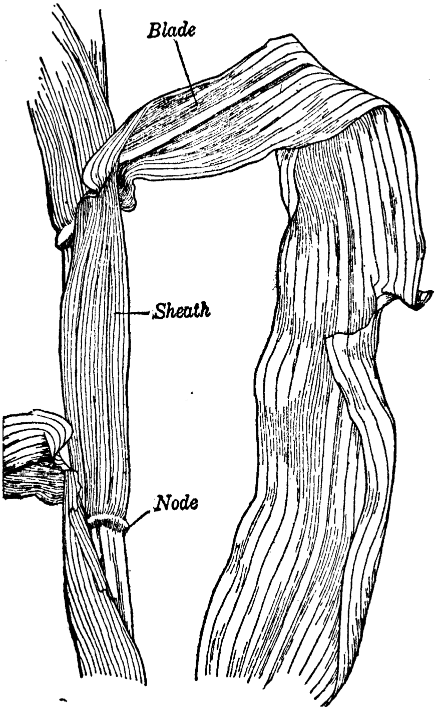


FIG. 3. Leaf of the corn, showing the sheath and a portion of the blade, and the arrangement of veins.

The primary root of a corn plant, like the primary root of a sunflower, is a direct continuation of the stem. It does not, at least under ordinary conditions, give rise to secondary roots. Often this primary root dies early. In such a case the root system of the corn then consists chiefly of roots which have grown, not from the primary root as in the sunflower, but from the lower nodes of the stem. Many of these *adventitious roots* (§ 31) arise at the underground nodes; but others commonly grow from one or more of the aboveground nodes of the corn stem. Some of the adventitious roots that arise above ground extend downward into the soil, so serving as props to the stem; others remain too short to reach the surface of the soil. The roots of the corn, like its stem, do not undergo secondary thickening.

6. Functions of Organs. Two important functions of a root system are, in most cases, anchorage of the plant in the soil and absorption from the soil of substances that are needed by the plant. The substances so taken in must be transported to the parts of the plant above ground, so that the conduction of absorbed substances is also a part of the work of roots. The storage of reserve food, too, is a function of many roots, and this function is especially important in such thick roots as those of the carrot, radish, and beet. The chief functions of the stem, and of the branches (if any), are usually the conduction of materials from roots to leaves and from leaves to roots, and the support of the leaves, as well as of the flowers, in a position favorable to the performance of their work. The leaves are, in the majority of seed plants, the chief food-manufacturing organs; but some food is made also in the green parts of stem, branches, and flowers.

FIG. 4. A corn plant.

7. Adaptation. It was suggested in § 1 that in general a plant and its organs are so constituted that they are able to perform their functions successfully. It may be added that these functions can be performed most satisfactorily under the conditions, such as those of temperature, light, and moisture, to which the plant is ordinarily exposed. These facts are summed up by saying that the plant is *adapted* to its environment. Adaptation in this sense is widely characteristic of living organisms, whether plants or animals. Adaptation is never perfect; but if organisms were not fairly

well adapted to their environment, obviously they would not long survive; nor will they usually survive if the environment is greatly altered. How the adaptation of organisms to their environment has come about is one of the major biological problems. Something of what is known regarding this problem will be discussed in Chapters XXXII and XXXIII.

CHAPTER II

THE STRUCTURE OF A CELL

8. Units of Structure. Every plant and every organ of a plant is made up of small parts, each of which is a *cell.* Cells are the units of structure of plants and animals, much as bricks or stones may be the units of structure of the wall of a house. As we must know the nature of bricks or of stones in order to understand the strength and durability of the house which is built of them, so to understand the nature of a plant or of an animal we must know something of the cells of which it is composed. Some very simple organisms consist each of a single cell; but in general any one of the larger plants and animals is composed, like the sunflower, of many cells too small to be seen with the naked eye.

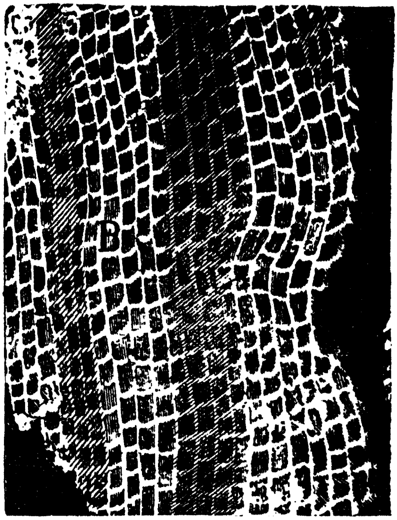


Fig. 5. The cellular structure of cork. This, the first published illustration showing a tissue composed of cells, appeared in Hooke's "Micrographia" in 1665.

The word *cell* commonly means a cavity or chamber which may be quite empty. But in speaking of the cells that compose a living organism, the word is used in a different sense. These units of structure were first called cells by Robert Hooke (1635–1703). Hooke was interested in examining various objects with the aid of the compound microscope, then a new toy, very crude as compared with present-day instruments, which had recently been introduced into England. Among other objects, as reported in his "Micrographia" (1665), he examined a thin slice of cork and, much to his surprise, found that it contained many little "pores

or cells" (Fig. 5). Years later it was recognized that cork, such as Hooke had studied, is made up of the walls of dead cells, and that the really living part of any cell is the liquid or jelly-like substance within its walls. Indeed, as is now known, many cells consist entirely of this liquid or semi-liquid substance and have no walls at all. However, the name *cell* has persisted and is applied to all these units of living matter, whether or not they are surrounded by walls.

Although the mature cells present in a plant are alike in fundamental characteristics, they may differ greatly in size, form, and function. The cells of any organ (such as a root, stem, or leaf) are organized into *tissues.* A tissue may be composed of cells all of which are much alike. However, the term *tissue* is also often applied to groups of cells which differ in structure but which coöperate in the performance of a common function. Thus, a root or stem contains conducting tissues each composed of cells of several different sorts as to size and form. Just as every plant, except some of the simpler ones, is composed of organs, so these organs are made up of tissues, and the tissues in turn are composed of cells.

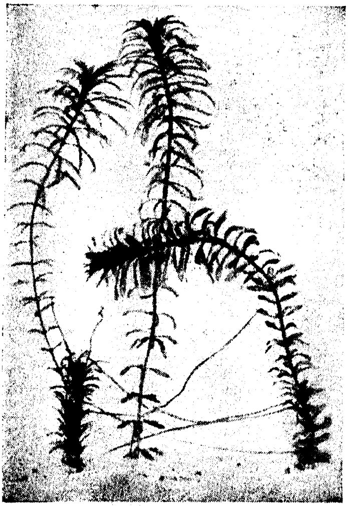


Fig. 6. Elodea plants.

9. Organization of a Cell. In the study of the living cells of one of the more complex plants, serious difficulty results from the fact that an organ of such a plant is usually of considerable thickness and composed of numerous cells. The microscope gives at best only a confused idea of any of the individual cells in such an organ. For this reason the cells can often be seen more clearly in a leaf, because of its thinness, than in a stem or root, and the thinner the leaf the more distinctly can the structure of an individual cell be made out. A favorable leaf for such a study of a mature cell is that of *Elodea* (Fig. 6), an aquatic plant sometimes called the "water pest," a native of North America which grows in sluggish streams and in ponds throughout the

continent, except in the extreme northern portions. The plant has a slender, branching, submerged stem varying in length, according to the depth of the water in which it grows, from a few inches to several feet. Slender roots growing from the stem anchor the plant more or less firmly in the soil at the bottom of the water. The many leaves are small, narrow, and pointed, and are usually borne in circles of three, four, or more.

A leaf of Elodea is only one cell in thickness at its margin, and for the greater part two cells in thickness elsewhere. Viewed from above (Fig. 7), the cells of several rows near the margin of the leaf appear narrow and rectangular. At intervals, pointed cells project from the edge. Occupying the greater part of the surface of the leaf are a larger number of rows of wider and shorter cells which, as will be seen later, are concerned largely in food-manufacture. The cells of the lower layer are about half as wide as those forming the upper layer. In the central portion of the leaf are several layers of narrow, elongated cells which constitute the midrib. Although a cell appears rectangular or square when seen under the microscope (which shows only one plane), it must be remembered that the cell has thickness as well, and is therefore box-shaped.

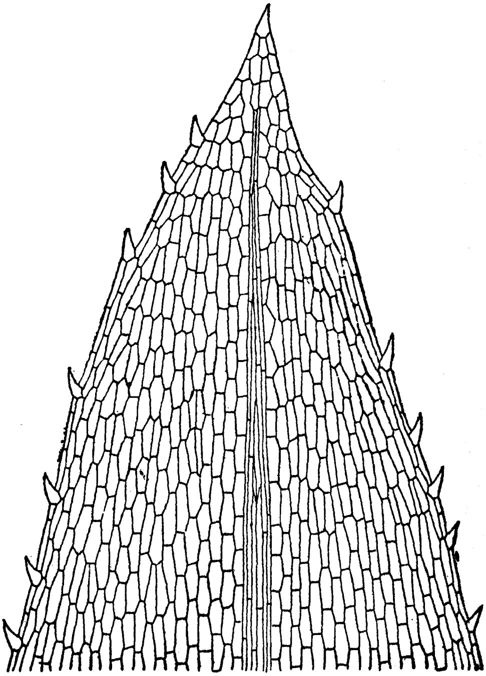


FIG. 7. Portion of an Elodea leaf.

The cells of the leaf (Fig. 8) are separated from one another, as well as bounded above and below, by transparent *cell walls.* The wall between any two adjacent cells is composed of several layers, of which the middle one is the oldest; during the

development of the cells the other layers were deposited successively on either side of this original layer through the activity of the living matter adjoining the wall on either side.

All the material within a cell wall is referred to as *protoplasm.* Protoplasm is never homogeneous; it consists of numerous substances differing in nature, which have a definite arrangement within the cell. The whole structure made up by the protoplasm—

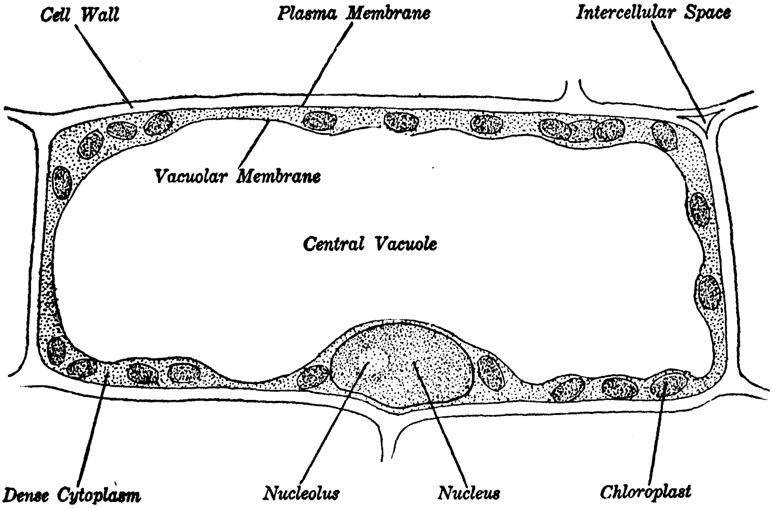


FIG. 8. A living cell of a leaf of Elodea, as seen in optical section.

that is, the body of the cell exclusive of the wall—is sometimes called the *protoplast.* The protoplasm is divided into *cytoplasm* and *nucleus.* Each of these two main divisions is in turn composed of various different substances which are definitely arranged. The arrangement of the substances that compose cytoplasm and nucleus is the *organization* of the cell. Because cells, as well as plants and animals which consist of many cells, have a definite organization, a single cell living alone, or a many-celled plant or animal, is an *organism.*

10. Structure of Cytoplasm. Just within the wall on all sides of a mature cell, including top and bottom, is a thin layer of the cytoplasm which appears relatively dense and often finely granular; this thin layer will be referred to as the *dense cytoplasm.* Included in it are many ovoid, or at times somewhat flattened, green bodies, the *chloroplasts.* These, which are also parts of the

dense cytoplasm, are the most conspicuous structures in most of the cells of a leaf. In the central part of the cell, enclosed by the layer of dense cytoplasm, is a large, transparent *central vacuole.* The *cell sap* which fills the central vacuole is a rather dilute solution of food substances, salts, and numerous other materials. The very outermost film of the dense cytoplasm, next the cell wall, is the *plasma membrane;* a similar film next the central vacuole is the *vacuolar membrane.*

Under certain conditions the layer of dense cytoplasm with the chloroplasts (but not including the plasma membrane) is in motion. The movement is mainly one of rotation (Fig. 9), usually about

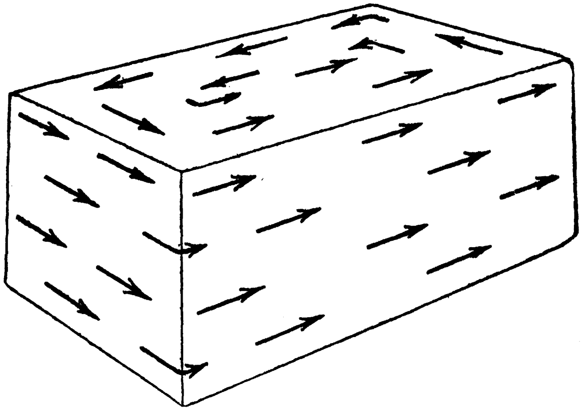


FIG. 9. Diagram showing the direction of rotation of the layer of dense cytoplasm in a cell of an Elodea leaf.

the vertical axis of the cell. Commonly the movement is in the same direction in all the cells of a leaf; but frequent exceptions to this rule occur. Occasionally a cross strand of dense cytoplasm cuts from one side to another through the central vacuole. The dense cytoplasm is the active substance in this movement; the chloroplasts are carried along by the current, much as pieces of ice may be carried in a river. The cell wall is perforated by pores, usually too minute to be seen with the highest powers of the microscope. These pores offer means by which the protoplasts of adjacent cells are either continuous or in contact with one another.

The similarity in color and in transparency between most parts of the cytoplasm, such as the dense cytoplasm and the

vacuoles, makes it impossible to distinguish accurately the boundaries of these parts when a cell is alive. On account of these difficulties it is necessary, in order to study the finer details of structure, to subject a leaf to a rather lengthy series of processes. These processes are, in brief: (*a*) killing and fixing the leaf in a poison or combination of poisons so selected as to kill the cells at once but to leave all parts of each cell in as nearly their original positions as possible; (*b*) hardening by means of alcohol; (*c*) cutting into thin sections; and (*d*) staining of the sections. The stains used in the last-named process are, with a few exceptions, aniline dyes. Advantage is taken of the fact that protoplasmic substances in general show an affinity for aniline dyes, and that different parts of the protoplast have varying affinities for different dyes. If, therefore, a section of a leaf is subjected to the successive action of two or three properly selected dyes of different colors, various parts of the cell may take on contrasting colors and thus stand out distinctly one from another.

The appearance of a cell in an Elodea leaf treated as just described (Fig. 10) is very different from that of a cell in a living

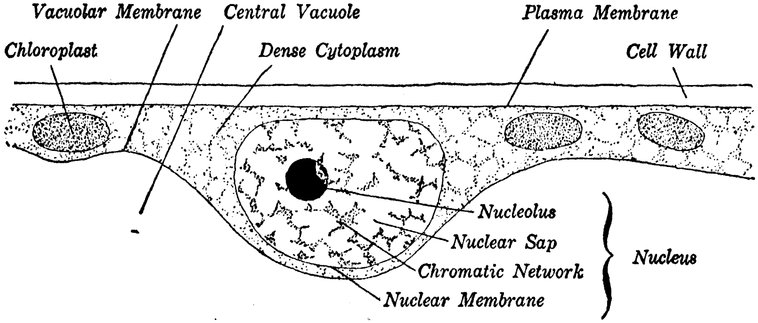


FIG. 10. Portion of a cell from a leaf of Elodea, after it has been killed and stained. Highly magnified.

leaf. The dense cytoplasm is seen not to be so nearly homogeneous as it appears to be in a living cell. Included in it are many clear vacuoles, varying greatly in size and shape but all very small; between these is a somewhat more deeply stained, often finely granular substance. In addition to vacuoles, chloroplasts, and minute granules, the dense cytoplasm includes bodies of varied form, smaller than the chloroplasts, which may be deeply stained.

These small cytoplasmic bodies (*chondriosomes*) are more readily observable in a young than in a mature cell (see Fig. 15).

When the cell is living, each vacuole contains a transparent liquid and is surrounded by a thin membrane; the granular substance between the vacuoles is also a liquid, but one of different nature. The visible structure of the dense cytoplasm is therefore that of an emulsion.

11. Structure of a Nucleus. A nucleus is an approximately hemispherical, semi-transparent body, imbedded like the chloroplasts in the layer of dense cytoplasm, and therefore close to the cell wall. In a living cell the nucleus appears to be homogeneous, except that it includes one or more fairly large, rounded refractive bodies, the *nucleoli.* The nucleus may be carried along by the cytoplasmic current, as the chloroplasts are, but more slowly. Consequently, at any moment it may lie at one side, at the top, or at the bottom of the cell.

In a living cell the nucleus is barely distinguishable from the dense cytoplasm in which it is imbedded. In a killed and stained cell the nucleus, because of the strong affinity of some of its parts for dyes, is the most conspicuous portion. Staining demonstrates also that the nucleus is not homogeneous in structure but is itself composed of parts differing in nature. It is bounded by a *nuclear membrane,* a film similar to the plasma and vacuolar membranes. Within the nucleus is usually at least one large, rounded, deeply stained nucleolus; some nuclei contain two or several nucleoli. There is also a network composed of material that is deeply stained but distinct from the nucleoli. Because it stains readily, this will be spoken of as a *chromatic network.* Its component strands vary in thickness; at the angles where they meet are granules or knots of varying sizes. As will be seen later (Chap. XII), the substances composing this network perform functions of very great significance. The chromatic network, and the nucleolus or nucleoli, lie in a *nuclear sap* which is usually unstained.

12. Nature of a Living Cell. All the protoplasmic structures that have been described, including those of both cytoplasm and nucleus, together constitute a living cell. Living cells are distinguished from non-living forms of matter by certain activities or processes that go on within them. It is not possible to define *living matter* so sharply that we can say that certain parts of the

protoplast are living and that other parts are non-living. So far as is known at present, the processes that distinguish living matter from non-living matter are carried on within cells which are organized in general much like those of an Elodea leaf. It is possible to say, also, that these processes which characterize living things have their seat primarily in certain portions of each cell—particularly in the dense cytoplasm including the plasma and vacuolar membranes, in the chloroplasts, and in the chromatic network of the nucleus. To this extent, the parts of the protoplast just mentioned are more living (or more actively living) than such other parts of the cell as the wall, the cell sap, and the nuclear sap.

Summary

A mature cell, such as one in a leaf of Elodea, consists of the following parts:

1. Wall:
   - Middle layer.
   - Later-formed layers.
   - Minute pores.
2. Protoplasm:
   - (*a*) Cytoplasm:
     - Dense cytoplasm:
       - Plasma membrane.
       - Small vacuoles, each with its membrane.
       - Intervacuolar substance.
       - Vacuolar membrane (next the central vacuole).
       - Chloroplasts.
       - Chondriosomes.
     - Central vacuole, containing cell sap.
   - (*b*) Nucleus:
     - Nuclear membrane.
     - Nucleolus (or nucleoli).
     - Chromatic network.
     - Nuclear sap.

CHAPTER III

HOW MATERIALS ENTER AND LEAVE A CELL

13. Elements and Chemical Compounds. The substances composing a plant, while of very many different kinds and degrees of complexity, are yet, like all substances, made up of *molecules*, and their molecules are composed of relatively few chemical *elements*. When a molecule of water is broken up into its constituent parts, each component is an *atom* of an element. A molecule of water is composed of two atoms of hydrogen and one atom of oxygen. In this case two gases have united to form a chemical compound that at ordinary temperatures is a liquid. The chemical formula for water, H_2O, indicates the elements of which it is composed and the proportion in which the atoms of those elements are present. Water is one of the simpler chemical compounds, and is of universal occurrence in living matter.

Among the compounds found in plants, while some such as water are relatively simple, a great number are composed of three or more elements each, and their molecular structure is vastly more complex than that of water. Of the compounds that are found in and manufactured by plants, many, which are characterized by containing the element carbon, are spoken of as *organic* in contrast to *inorganic compounds*. Inorganic compounds occur in nature independently of the activities of living matter, but many of them are absorbed and used by plants.

14. Diffusion. Before discussing the passage of substances into and out of a living cell, it is necessary to consider *diffusion*, a process that is very largely involved in such movements.

If ether is poured into an open vessel, the odor soon indicates that the ether is becoming distributed through the air of the room. Liquid ether is composed of a vast number of molecules which are relatively close together and all in vigorous motion. Because of their comparatively crowded condition the molecules are constantly in collision, striking one against another and rebounding. At the free surface of the liquid opportunity is greatest for the movement of the molecules. Hence many of them, when

they reach this surface, fly off into the air. Having passed into the air, they are still in motion and tend to distribute themselves uniformly through the available space—that is, through the room. The liquid ether thus rapidly becomes a gas. The change of ether from a liquid to a gaseous state is a consequence of the tendency of its molecules to become uniformly distributed throughout the space available. The process of distribution which results from this tendency is *diffusion.* A tendency to diffuse characterizes all matter.

The space within the room into which the ether molecules pass is filled with air, a mixture of rapidly moving molecules of gases, those present in largest amounts being oxygen and nitrogen. When molecules of ether pass into the air, they tend to diffuse uniformly among the molecules of oxygen, nitrogen, and other gases that may be present. The diffusion of each gas throughout the space available is independent of the diffusion of each of the other gases. The consequence is that all the gases within a limited space, such as a room or a small container, will in time become so distributed that a uniform mixture will result.

The same principle may hold when two or more liquids are in contact. For example, if liquid ether and alcohol are brought together in a dish, the alcohol diffuses throughout the ether, the final result being a homogeneous mixture. Just as diffusion may occur between gases or between liquids, so there may be diffusion between gases and liquids. For example, if oxygen and water are in contact, a certain proportion of oxygen diffuses into the water. However, the water is just as truly diffused through the oxygen as is the oxygen through the water.

Similarly, a solid substance may diffuse through a liquid. A small amount of sugar or common salt in contact with a sufficient amount of water disappears, so that neither by the naked eye nor under the microscope can any evidence of the presence of the solid be detected. The mixture is homogeneous in character. If the solid is added bit by bit the result is similar, the mixture remaining homogeneous throughout the operation. Finally, however, when enough of the solid is added, the process of mixing appears to stop; some of the solid settles to the bottom, and the mixture is no longer homogeneous.

Not all substances, when brought together, diffuse readily into one another. Olive oil and water, for instance, when in contact

diffuse into each other but very slightly; the two liquids remain substantially separate. Whether or not substances will diffuse into one another depends upon their respective natures.

When a solid or a gas diffuses into a liquid, the resultant homogeneous mixture is spoken of as a *solution.* The liquid is the *solvent,* the substance diffusing into it the *solute.* When two liquids are concerned in the process, one of which is water, the water is commonly considered the solvent. It would be equally possible, however, to consider the other liquid, for example alcohol, as the solvent and the water as the solute.

Water possesses the property to a remarkable extent of dissolving other substances; in fact, a greater variety of substances are dissolved by water than by any other known liquid. In living cells the principal solvent is water; the solutions that occur in plants are chiefly solutions of solids, liquids, and gases in water.

It is important to note that the diffusion of any solute through water is independent of the diffusion of any other solutes present; in a solution of sugar and common salt the diffusion of the sugar is independent of that of the salt. The capacity of different substances to dissolve in water is extremely variable. For example, very large proportional amounts of sugar and salt will dissolve in water; only slight amounts of iron and some other metals will so dissolve. Some substances, like camphor, which are practically insoluble in water, are readily soluble in some other liquids such as alcohol or ether. The solubility of any substance in a liquid depends, then, upon the nature both of the solvent and of the solute. Surrounding conditions also influence solubility. For instance, changes of temperature affect the solubility of a solute in water. As a rule, solids become more soluble in water, and gases less soluble, as the temperature is raised. The solubility of some substances in water increases rapidly with a rise in temperature, while for other substances the increase is slow.

15. Osmosis. If two substances which tend to diffuse are separated by a membrane through which both separated substances can readily pass, they will still diffuse despite the presence of the membrane. Thus if water and a solution of sugar in water are placed in the respective arms of a U-tube and are separated by a partition of rather coarse cloth, the sugar will pass through the cloth and diffuse in the water on the other side of the partition; the water will pass through the partition in the opposite

direction. In time there will be a homogeneous mixture of sugar and water of equal concentration on both sides of the partition. In this case the membrane is *permeable* to both sugar and water.

If the water and the solution of sugar are separated by a rubber membrane, neither water nor sugar will diffuse through the membrane. In this case the membrane is *impermeable* to both sugar and water.

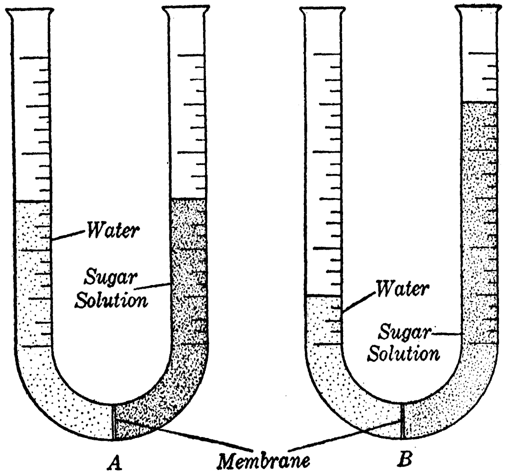


FIG. 11. An apparatus illustrating osmosis. *A*, at the beginning of the experiment; *B*, after standing for a time. One arm of the U-tube containing pure water is separated by a differentially permeable membrane from the other arm, containing a sugar solution. Note in *B* the rise of the liquid in the arm containing the sugar solution.

If the water and sugar solution are separated by a membrane of parchment paper, the water will pass more rapidly through the membrane into the sugar solution than sugar will pass into the water, and the liquid will rise in the arm of the tube containing the sugar solution (Fig. 11). Although the membrane is permeable to both water and sugar molecules, it is permeable to them in different degrees, sugar diffusing through it slowly and water more rapidly. The membrane differentiates between the two substances. In this case the membrane is *differentially permeable* to sugar and water.

The same principle may be illustrated by the use of a thistle tube (Fig. 12) over whose lower end parchment paper is fastened tightly. A fairly concentrated solution of sugar is placed in the lower end of the tube, which is immersed in water. Water will diffuse through the differentially permeable membrane into the sugar solution. Some of the sugar will diffuse very slowly through the membrane into the water. Since the water diffuses more rapidly than the sugar, the result will be a rise of the solution in the tube.

If a differentially permeable membrane separates aqueous solutions of two different substances (for example, a solution of sugar and one of salt), ordinarily water will at first diffuse chiefly from the less concentrated to the more concentrated solution. Precisely what will happen, however, depends upon the nature of the membrane, the nature of the solvent, and the natures and relative concentrations of the solutes.

The diffusion of a gas, a liquid, or a dissolved substance through a membrane is commonly called *osmosis.* The direction of the major osmotic movement of any substance is determined by the relative number of particles of that substance present. In general, the direction of movement is from the side of the membrane where the proportional number of particles of the diffusing substance is higher to that side on which the proportional number is lower. A diffusing substance may be moving in both directions through a membrane, but more particles of that substance are moving away from the side where they are proportionally more numerous than from the side where they are less numerous. Unless prevented, the movement will continue until equilibrium is established.

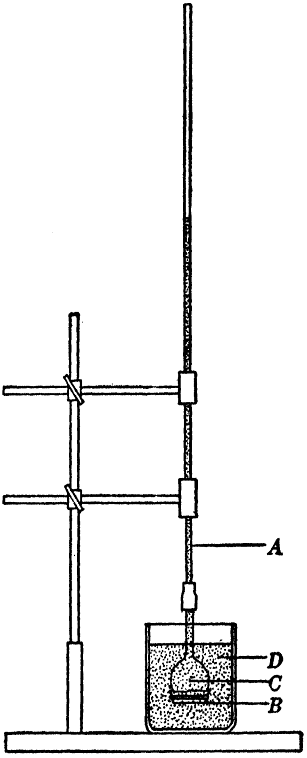


FIG. 12. An apparatus to illustrate osmosis. *A*, a thistle tube whose lower end is closed by the differentially permeable membrane *B*. The lower end (*C*) of the tube contains a concentrated sugar solution. The vessel *D* contains water.

16. Significance of Osmosis. A cell such as one of the Elodea leaf is an osmotic apparatus shut off from the outside world, and largely from adjoining cells, by a cell wall and a plasma membrane. Both are differentially permeable, but the wall permits the ready passage of many more substances than does the plasma membrane. In consequence, it is the plasma membrane which chiefly determines what substances shall enter or leave the cell. When substances entering the cell have once passed the wall

and the plasma membrane, their further movement within the cell is regulated by a variety of other membranes. If substances are to reach the central vacuole they must pass the vacuolar membrane, which is itself differentially permeable. In a general way, whether or not a particular substance is to enter or leave a cell depends upon the relative concentration of that substance in the central vacuole and in the liquid outside the cell. The transfer of substances between cytoplasm and nucleus is regulated by the nuclear membrane, which is also differentially permeable.

Under ordinary conditions the solutes in the cell sap are more concentrated than are those in the liquid surrounding the protoplast. In consequence, water passes by osmosis into the cell.

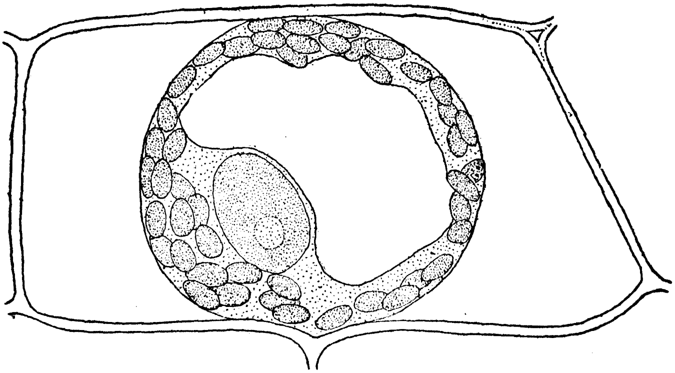


FIG. 13. A cell showing plasmolysis resulting from immersion in a strong solution of common salt.

Continued movement of water into the protoplast results in a pressure within the vacuoles. This pressure is sufficient to distend the protoplast as far as the elasticity of the wall will permit. The pressure thus developed within the cell is called *turgor* and the cell is said to be *turgid.* A cell may be more or less turgid according to the amount of pressure within.

If the concentration of the solutes in the liquid outside the protoplast is greater than the concentration of those in the cell sap, water will be withdrawn from the protoplast by osmosis. A sufficiently extensive withdrawal of water from the protoplast reduces the pressure to such a degree that the protoplast is partially or entirely withdrawn from the wall and becomes more or less rounded. In this state of contraction the cell is said to be *plas-*

molyzed. The process of becoming plasmolyzed is *plasmolysis.* Plasmolysis may be illustrated by placing a living leaf of Elodea in a rather strong solution of cane sugar or of common salt (Fig. 13). Prolonged plasmolysis is usually fatal to a cell. If, however, a leaf in whose cells plasmolysis has not proceeded too far is removed from the sugar or salt solution and placed in approximately pure water, water will diffuse inward and the cells will return to their former turgid condition.

The absorption of substances concerned in the nutrition of a plant depends largely upon osmosis, since all substances that enter or leave any living cell must be either liquid or dissolved and must be capable of diffusing through the plasma membrane. Water and a vast number of dissolved substances with which the activities of a cell are concerned diffuse into or out of the cell independently of one another. Water and dissolved substances may enter or leave a cell at the same time at very different rates, some of them passing inward and others outward. The structure and composition of living membranes are important in determining what substances shall enter or leave a cell. While a plant is alive the permeability of any living membrane, such as a plasma membrane, may vary greatly from time to time; the variations depending upon numerous conditions internal and external to the cell, including age, temperature, and light. At one time a membrane may be readily permeable to a particular substance; at another, relatively impermeable to the same substance. It is true also that there are great differences in permeability between the plasma membranes of different cells, the differences often being extremely great in this respect between cells of the same plant.

Osmosis plays an important part in the transport of water and dissolved substances from cell to cell and from organ to organ, in the absorption of gases from the atmosphere by the cells of leaves and of other organs, and in the absorption of water and of other substances in solution from the soil by the cells of roots. The turgidity of cells is important in maintaining the rigidity of certain parts of plants, such as leaves, young stems, and young roots. The form, and especially the position, of non-woody plants and parts of plants depend largely on the turgidity of their cells. A loss of turgidity by the cells of such plants results in their wilting.

17. Imbibition. Osmosis explains in large part how water and dissolved substances enter the living protoplast. Another process

which plays a part in the passage of liquids and dissolved substances into the cell walls and thence into the protoplast, is *imbibition.* A familiar illustration of imbibition is the soaking up of water by dry gelatine or wood. The absorbed water is drawn into the spaces between the particles that make up the gelatine, or into similar spaces in the walls of the cells that make up the wood. The water eventually becomes so arranged about the particles of such a substance that it forms films which crowd the particles of the imbibing substance apart and this substance swells. The extent to which the particles can be forced apart by the water depends upon the cohesion between the particles of the imbibing substance. In the case of gelatine, its particles may become so widely separated by the water that the mixture becomes a liquid. In the case of wood the limit of the separation of its particles is soon reached. Water is imbibed readily by the walls of living cells, except those of certain tissues which are impregnated with fat-like substances. In a cell of the Elodea leaf, the process of imbibition brings water and dissolved substances into contact with the plasma membrane. It is then possible for these substances to enter the protoplast either by osmosis or by imbibition, since the plasma membrane is capable of imbibing water and some dissolved substances. The differential permeability of the plasma membrane is thus determined in part by the readiness with which it imbibes certain dissolved substances and by its inability to imbibe others. Imbibition and osmosis are closely related processes; osmosis is made possible by the imbibing powers of the cell wall and of the plasma membrane. Some plant cells, especially those of certain desert plants, contain substances of a mucilaginous nature. These substances, located in the vacuoles, in the dense cytoplasm, or in both, by their power of imbibition increase the water-absorbing and water-holding capacity of the cells containing them, to such an extent that the cells resist long periods of drought.

18. Suction Tension. The processes of osmosis and imbibition just discussed, together with other processes which may play a minor rôle, result in a tendency on the part of every healthy protoplast to draw in water, leading to the production of a *suction tension.* This suction tension is important not only in the activities of a living cell but also, as will appear in later chapters, in the transfer of water and dissolved substances throughout a plant.

Summary

Chemical compounds found in plants are composed of relatively few elements. The inorganic compounds are relatively simple; the organic compounds are more complex.

Diffusion results from the tendency of molecules to become equally distributed, as illustrated by the mixing of two gases, of a gas and a liquid, of two liquids, or of a solid and a liquid, to form a homogeneous mixture. The mixture of a gas and a liquid, of a solid and a liquid, or of two liquids is a solution. The liquid involved in a solution is the solvent, the other substance the solute. If two liquids are concerned one of which is water, the water is commonly considered the solvent. Solutions occurring in plants are chiefly of solids, liquids, and gases in water. Solutes in water diffuse independently of one another, but the process is affected by the nature of the solute. Temperature affects solubility, solids as a rule becoming more soluble, gases less soluble, as the temperature rises.

Osmosis is diffusion through a membrane. The rate of osmosis varies with the nature of the membrane, of the solvent, and of the solute, with the concentration of the solute, and with the temperature. Permeable membranes allow both solvent and solute to diffuse with little hindrance; impermeable membranes are permeable neither to solvent nor to solute. A differentially permeable membrane is permeable to both solvent and solute but to different degrees.

A living cell is enclosed by a cell wall and a plasma membrane, both of which are differentially permeable. Because of its lesser permeability to solutes, the plasma membrane chiefly determines what substances shall leave or enter the cell by osmosis. Since solutes are ordinarily more concentrated within a protoplast than in the liquid outside the cell, water passes into the protoplast by osmosis and develops a pressure (turgor), causing the cell to become turgid. If the conditions just mentioned are reversed, water is withdrawn and the protoplast is plasmolyzed.

The structure and composition of living membranes are important in determining what substances shall enter or leave a cell. The permeability of living membranes varies from time to time, depending upon conditions within and without the cell such as age, temperature, and light.

Osmosis is important in the transport of water and dissolved substances within the plant and in the absorption of substances in solution from the soil by roots. The form of a non-woody plant is maintained largely by the turgidity of its cells.

Imbibition plays an important part in the absorption by cell walls of water and dissolved substances, bringing these substances into contact with the plasma membrane through which they may pass by imbibition and osmosis. The protoplasts of some plants contain substances which imbibe and hold large quantities of water, enabling them to endure periods of drought.

Every healthy protoplast possesses a suction tension, resulting from its tendency to take up water by osmosis and imbibition. Suction tension is a factor not only in the absorption of water, but also in the transfer of water and dissolved substances.

CHAPTER IV

ROOTS

19. Regions of a Root. The roots of a sunflower are representative of the type of roots normally growing in soil. Their structure is particularly suited for the performance of their principal functions: anchorage, the intake of water and of other materials, and the conduction of these to the stem. Since little or no food material is stored in the root system of the common sunflower, there are no prominently thickened portions except for the enlarged primary root. From this arise many smaller secondary roots, which in turn are branched and rebranched. These smaller roots, extending downward and outward, hold the plant firmly in place and provide a large absorbing area.

The extreme tip of a root (Fig. 14) is covered by a *root cap*. A root as a whole, exclusive of the root cap, may be thought of as divided into four general regions which merge gradually one into the other. These regions are, beginning back of the cap: the formative or *embryonic region*, in which cell division takes place; the *region of elongation*, in which the cells grow, chiefly in length; the *region of maturation*, in which the various cells take on the characteristics distinctive of particular tissues; and the *mature region*, in which cells have become definitely differentiated, structurally and functionally. In consequence of the continued growth and maturation of cells formed in the embryonic region, as well as of cells formed by occasional divisions in the region of elongation, the length of the root is steadily increased and the root tip is pushed farther and farther into the soil.

20. Root Cap. The cells of the root cap, like those in other parts of a root, are formed by divisions in the embryonic region. Beginning at this region and progressing forward through the cap there are, successively, a short region of elongation, one of maturation, and, at the extreme tip and outer sides of the cap, a mature region. Since the cells in these three regions go through the same course of development, though in an abbreviated form, as do the cells in the corresponding regions of the main body of the root,

their history need not be followed in detail. The continued elongation and maturation of cells does not, however, add to the volume of the mature portion of the cap, since the middle layers of the walls between the outermost cells in the mature portion are constantly dissolving away and the cells are sloughing off as the elongating root forces the cap through the soil. The root cap serves to protect the embryonic region from possible injury as the root tip is pushed forward.

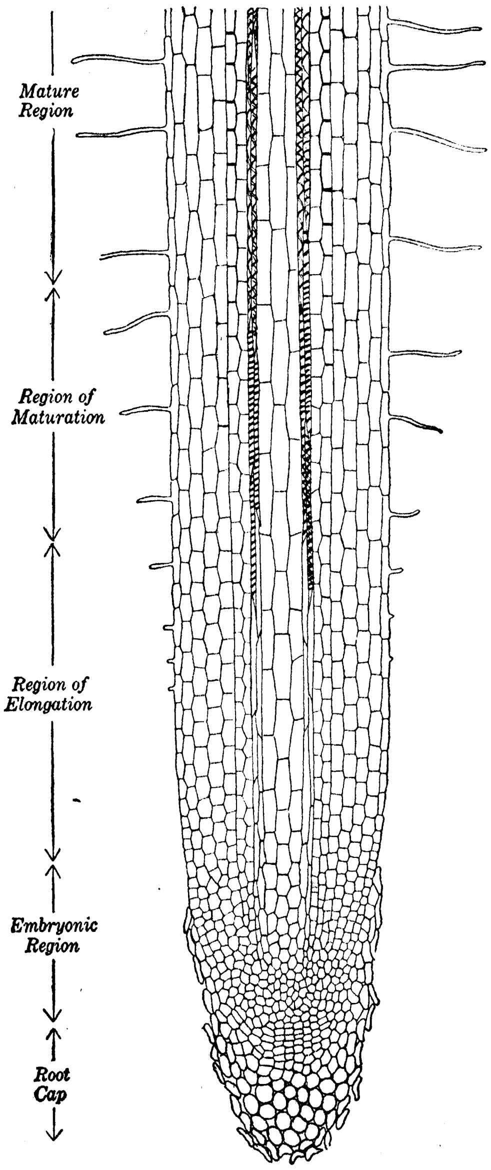


FIG. 14. Lengthwise section of a root tip (dia-

21. Embryonic Region. The embryonic region, unlike other regions of the root, is a substantially uniform tissue composed of small, closely packed, angular cells (Fig. 14). The cells in this region are distinguished from those of most other parts of the root by their capacity for indefinitely repeated division. Because of this capacity they are known as *embryonic cells.*

A section of a root treated as previously

that embryonic cells are different in appearance from mature cells. Since nuclear and cell division (Chap. XII) are likely to be going on in many of the cells in the embryonic region, it is necessary to select for the present comparison a *resting cell*—that is, one whose nucleus and cytoplasm are not in process of division.

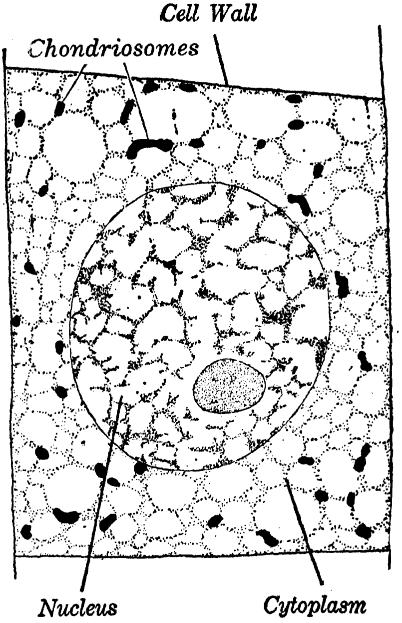


FIG. 15. An embryonic cell from a root tip of an onion.

In the first place, the wall of an embryonic cell (Fig. 15) is very thin as compared with that of a mature cell. Second, the embryonic cell contains no central vacuole. The space within the wall is occupied by a nucleus and dense cytoplasm, the latter containing many minute vacuoles and being similar to the substance of the peripheral layer in a mature cell. Third, the embryonic cell contains no chloroplasts. Among the small darkly stained bodies (chondriosomes) in the dense cytoplasm, however, are some which may develop into larger structures (*leucoplasts*) that in certain important respects resemble chloroplasts. Fourth, the nucleus is large in proportion to the size of the cell and lies in its central part. The nucleus of an embryonic cell, like that of a mature cell, is surrounded by a nuclear membrane and contains a nucleolus or nucleoli, a chromatic network, and nuclear sap.

The continued division of cells in the embryonic region would result, if nothing occurred to prevent, in a steady increase in number of embryonic cells and in the size of the embryonic region. No such increase occurs because the cells which come to lie in the anterior and posterior portions of the embryonic region cease to divide and begin to enlarge. These cells thus become constituents of the two regions of elongation—those, respectively, in the root cap and in the body of the root. The

volume of the embryonic region, therefore, remains approximately constant.

22. Region of Elongation. The cells which lie posterior to the embryonic region constitute the part of the body of the root that has been referred to as the region of elongation (Fig. 14). The cells in this region are enlarging, chiefly in length. As a cell enlarges, the amount of each of its component substances doubtless increases; but the largest factor in its enlargement is an increase in water content. Most of the additional water is taken into certain of the minute vacuoles that are scattered throughout the cytoplasm. The result is a great increase in size of these particular vacuoles (Fig. 16); the majority of the vacuoles, however, remain small. Now and then two or more of the enlarging vacuoles come into contact and coalesce. Gradually, therefore, the number of conspicuous vacuoles in the cell becomes smaller, and finally, in the cells of many tissues, all the growing vacuoles unite into a single large central vacuole. The coalescence of vacuoles results in pushing the rest of the cytoplasm to the outer part of the cell. This relatively thin layer just inside the wall is what was referred to in the description of the mature cell (§ 10) as the "dense cytoplasm." Since the numerous vacuoles that remain minute are included in it, the dense cytoplasm still has an emulsion-like structure. The nucleus remains imbedded in the dense cytoplasm, and is therefore finally located near the cell wall.

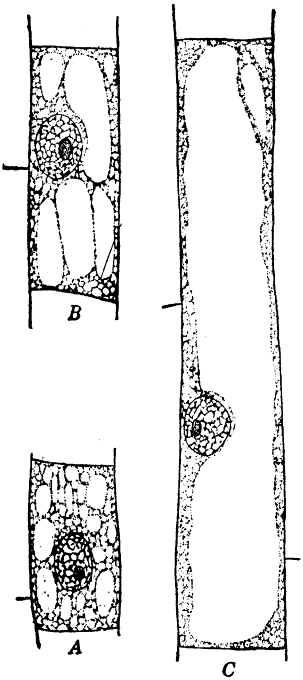


FIG. 16. Stages in the development of an embryonic cell to the mature condition.

It might be expected, since the enlargement of a cell is due largely to the absorption of water by certain vacuoles, that it would expand equally in all dimensions. This is not generally the case; for most of the enlarging cells of a root undergo a greater increase in length than in either lateral dimension.

All the cells of the embryonic region are substantially alike; but as they begin to enlarge differences appear. Certain groups of cells which are to constitute the respective tissues in the mature part of the root now begin to differ in size and shape. The majority of the cells in the axial portion of the region of elongation grow to many times their original length. The cells outside this central region grow to but three or four times their original length. Thus, even in the region of elongation it is evident that the mature region of the root will include a differentiated central portion (the *stele*) and a surrounding zone of different nature (the *cortex*).

23. Region of Maturation. The differences in size and shape first evident in the region of elongation become more apparent as the fully enlarged cells take on their mature characteristics (Fig. 14). In general, the walls of maturing cells become thicker by the formation of new layers of wall material. The original thin wall separating two adjoining embryonic cells, somewhat modified in thickness and in chemical composition, remains as the middle layer of the mature wall. As will appear, the cells of various tissues differ materially in the amount of thickening that their walls undergo and in the manner of deposition of the additional wall layers.

24. Mature Region. The mature portion of a root (Fig. 14) consists of three parts, concentrically arranged: stele, cortex, and epidermis. The innermost of these parts, the stele, is a solid cylinder. External to the stele and surrounding it is the cortex, several cells in thickness. The cortex, in turn, is ensheathed by the epidermis which is but one cell in thickness.

The cells of the young stele do not all mature into the same type of tissue. A cross section of a sunflower root cut at the posterior portion of the region of maturation (Fig. 17) shows that four (or more) groups of cells toward the periphery of the stele develop especially thick walls, constituting a tissue known as the *primary xylem*. Later the cells inward from these first-matured groups of primary xylem also mature into elements of primary xylem which are of larger diameter. When maturation is complete, the primary xylem often constitutes a mass that fills the entire central portion of the stele. Projecting outward from the central mass, as seen in cross section, are four or more radiating arms. These are sectional views of as many longitudinal ridges—the first-matured groups of primary xylem. The outer portions of these ridges are composed

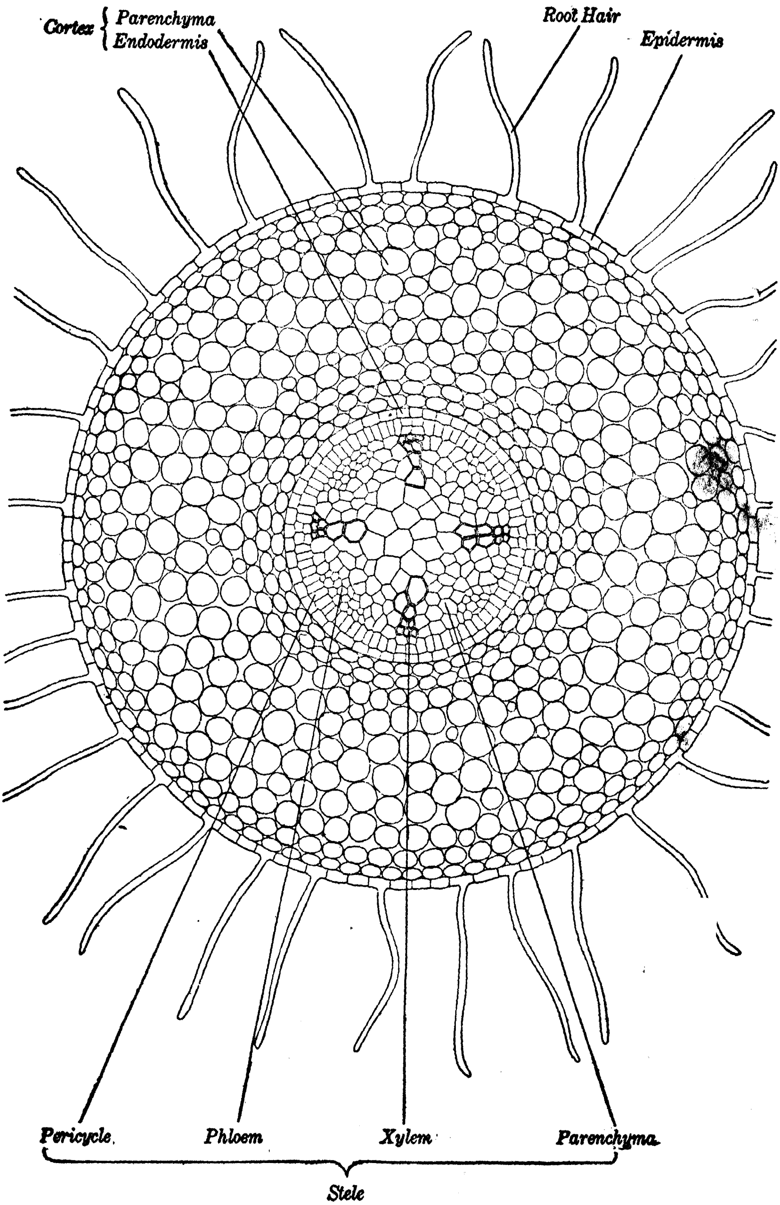


FIG. 17. Cross section of a sunflower root (diagrammatic) at a level at which cambial activity has not yet begun.

of elongated cells with pointed ends (*tracheids*, Fig. 18, *A*). During maturation the cell walls of young tracheids are thickened by the addition of new layers. In some tracheids the new layers are deposited upon a limited portion of the inner surface of the wall in the form of a spiral band that runs the whole length of the cell; in other tracheids the internal thickening takes the form of a series of rings which encircle the cell transversely. Cytoplasm and nuclei disappear from the tracheids after the formation of these additional wall layers. Mature tracheids, therefore, consist of cell walls only, and each is the result of the maturation of a single embryonic cell.

Many of the cells inward from those that become tracheids mature into *vessels* (Fig. 18, *B*). A vessel is an element resulting from the maturation of a vertical row consisting of a variable number of embryonic cells joined end to end. After the increase in length which these cells undergo in the region of elongation, their maturation begins with a great increase in the diameter of each cell of the row (Fig. 19, *B*). After this enlargement is completed, additional layers of wall material are deposited on the lateral walls of the cells. In the first vessels to mature, the additional wall material is laid down in transverse rings or in a continuous spiral. The thickened walls of later-matured vessels often contain many thin areas (*pits*) in which the material of the later-formed layers was not deposited. After the thickening of the lateral walls the cross walls between adjoining cells of the vertical row disappear, except for the outer margin of each cross wall. Finally the protoplasts disappear (Fig. 19, *D*). Hence a vessel is a tube formed from a row of originally separate cells; it differs in this respect from a tracheid, which is at all stages a

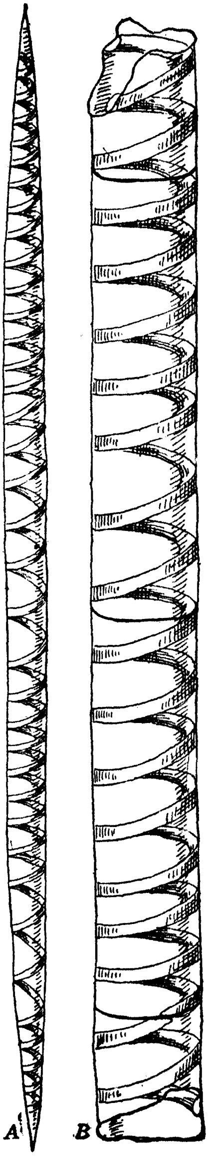


FIG. 18. *A*, a tracheid with spirally thickened wall. *B*, portion of a vessel with spirally thickened wall.

single cell. Tracheids and vessels are not functionless when mature, even though they lack protoplasts: as will appear in a later chapter, water passing through the root to the stem moves chiefly through these dead elements.

In the angles between the radiating ridges of primary xylem are groups of cells that mature into *primary phloem*. The alternate

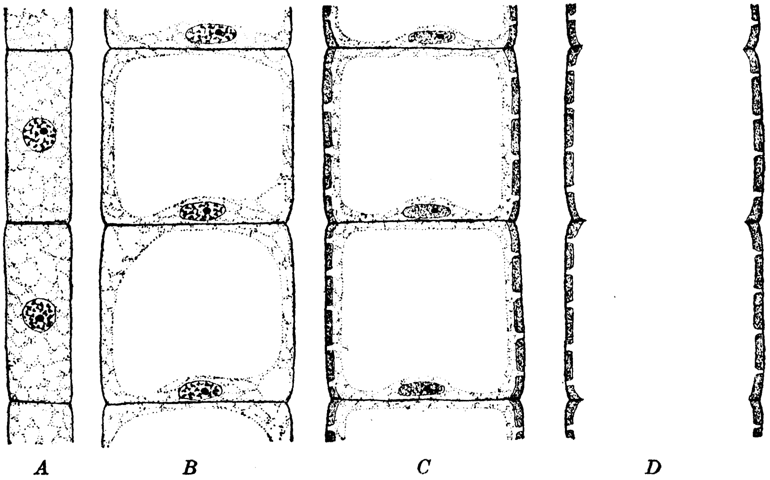


FIG. 19. Stages in the development of a vessel from a row of originally separate cells.

distribution of xylem and phloem groups in the peripheral portion of the stele is characteristic of young roots in general. The *sieve tubes* (Fig. 20) are the most conspicuous elements of the phloem. Each sieve tube is formed by the maturation of a vertical row of embryonic cells. It is called a "sieve tube" because the walls between adjacent cells in the row are perforated by groups of pores which, though small, are much larger than the minute pores referred to in § 10. In a lengthwise section a mature sieve tube appears as a series of elongated cells arranged end to end, with strands of cytoplasm extending through the pores. Manufactured foods, and possibly other materials, are moved through sieve tubes. Interspersed among the sieve tubes are other thin-walled cells whose walls do not develop pores; these cells, which may be long or short, contain cytoplasm and nuclei, whereas the nuclei of the sieve tubes sooner or later disappear. In the roots of some plants, though not of the sunflower, a narrow, elongated *companion cell*

lies beside each sieve cell—that is, beside each segment of a sieve tube.

Lying between the primary xylem and the primary phloem are many thin-walled cells. These, like the slightly elongated, usually thin-walled cells found elsewhere in root and stem, are *parenchymatous cells.* A tissue composed of such cells is a *parenchyma.* Surrounding the phloem and xylem, and appearing as a ring in cross section, is a sheath of parenchymatous tissue, the *pericycle.* It is in this outermost region of the stele that secondary roots originate.

Immediately outside the pericycle is a single layer of cells, the *endodermis,* which is the innermost region of the cortex. Early in the maturation of endodermal cells (in many plants), the middle part of each radial wall becomes thickened. Further deposition of wall material may result in a uniform thickening of the radial walls. In some plants, including some kinds of sunflower, there follows, in turn, a thickening of the tangential walls at the inner faces of the cells. The remaining portion of the relatively thick cortex is made up for the most part of rounded parenchymatous cells.

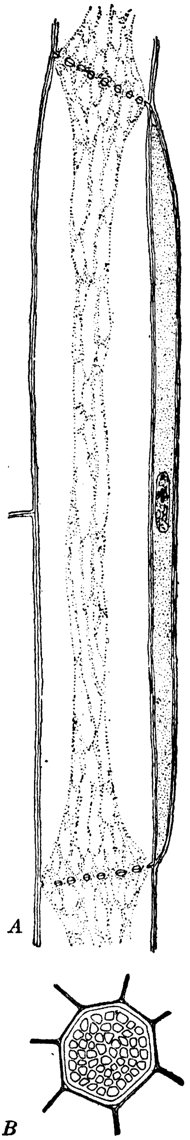


FIG. 20. *A*, lengthwise section of a sieve tube segment and its companion cell, from the secondary phloem of a root of the squash. *B*, the end wall of a sieve tube segment, showing a group of pores.

The surface layer of cells in the embryonic region of a root matures into a tissue, one cell in thickness, known as the *epider-*

mis. In the posterior part of the region of elongation, many of the epidermal cells develop long tubular projections from their outer sides. These projections, the *root hairs,* elongate to many times the diameter of the epidermal cells and thus increase very

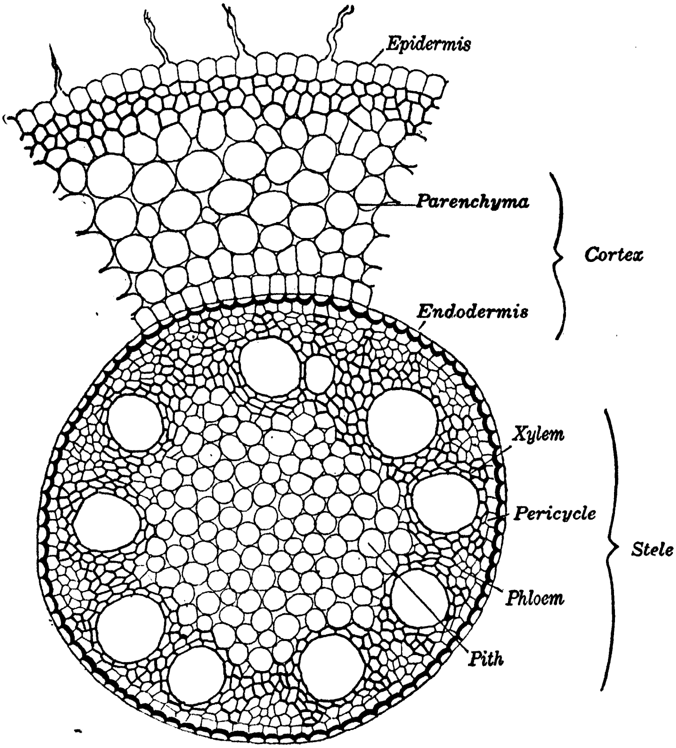


FIG. 21. Cross section of the stele and endodermis, and of a portion of the cortex of a corn root.

greatly the absorptive surface of the root. It is largely through the root hairs that water is absorbed from the soil, together with some other materials, chiefly mineral salts, which are dissolved in the soil water. This water passes from the root hairs through the cortex to the tracheids and vessels, whence it rises into the stem and is distributed throughout the plant. The length of the portion of a root on which root hairs persist extends back from the region of elongation for a variable distance, depending upon the species and upon the environment of the root. The number of root hairs

developed depends largely also upon the medium in which the root is growing. After they have ceased to function, either the root hairs remain in a shriveled condition or the epidermal layer with the root hairs is sloughed off. New hairs are formed only in the

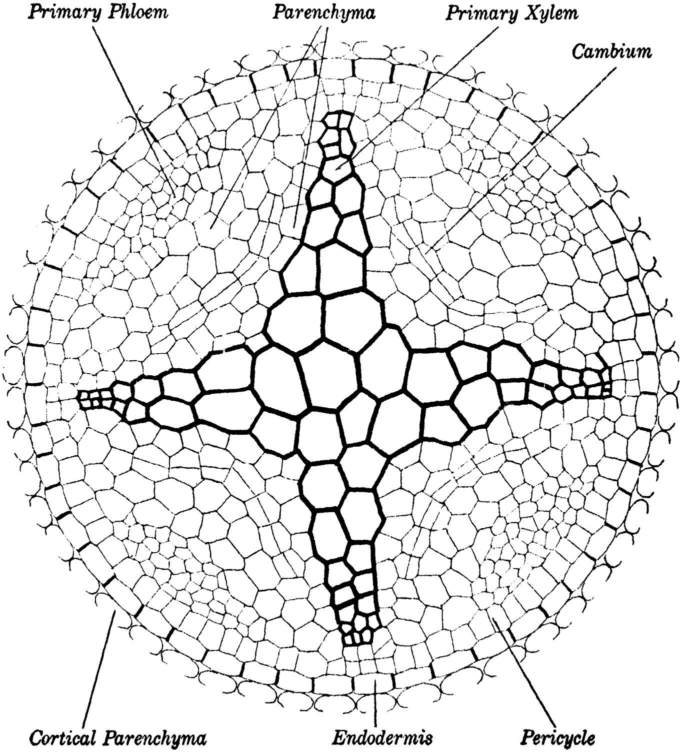


FIG. 22. Cross section of the central portion of a root (diagrammatic) at a level at which cambial activity is beginning.

elongating region of the root. Therefore, as the root penetrates farther into the soil its absorbing portion (that bearing root hairs) comes to be more remote from the stem.

25. Secondary Thickening. All the tissues thus far considered were formed by the maturation of cells produced by cell divisions in the embryonic region or, less frequently, in the region of elongation. Tissues produced by the maturing of such early-formed cells are termed *primary tissues* in distinction to *secondary tissues* which originate in a different manner.

Seed plants are divided into *gymnosperms*, among which are the pine, larch, and spruce; *dicotyledons*, including many trees, shrubs, and the majority of other seed plants; and *monocotyledons*, of which corn, wheat, and the lilies are examples. One respect in which monocotyledons differ from gymnosperms and dicotyledons

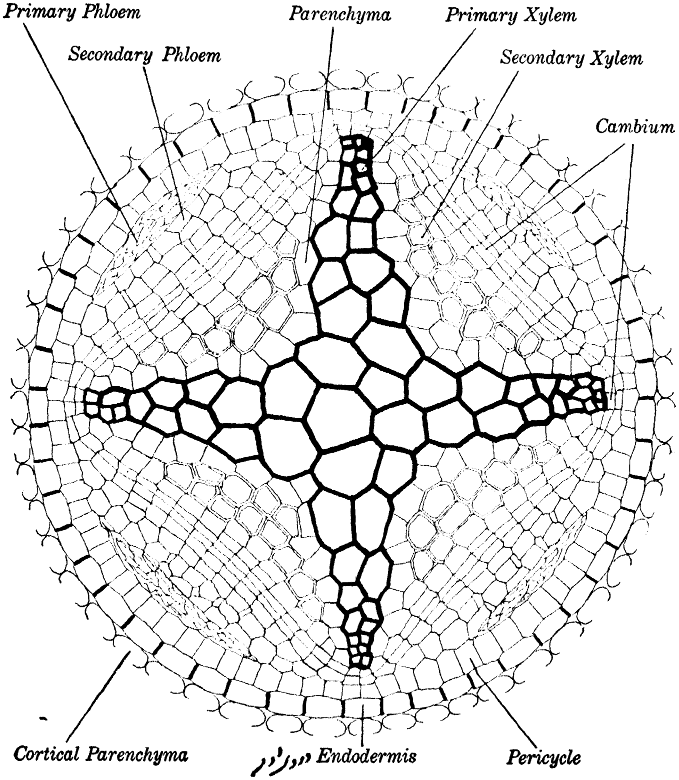


FIG. 23. Diagram of the central portion of a root after the formation of a continuous zone of cambium outside the xylem.

is that monocotyledons produce no secondary tissues in their roots, whereas the roots of gymnosperms and dicotyledons usually form secondary tissues.

The sunflower is a dicotyledon whose roots increase in thickness by the formation of secondary tissues. The production of secondary tissues in a sunflower root results from the activity of an embryonic tissue known as the *cambium*. First to function as cambium are certain cells lying just within each phloem group and outside the

central mass of xylem (Fig. 22). In a root with four phloem groups, therefore, four cambium regions appear. The cambial cells, although they have enlarged and changed more or less in structure, have nevertheless retained their embryonic character. Each one divides tangentially (that is, in a plane at right angles to the radius of the root) into two daughter cells. Further tangential divisions increase the diameter of each strip of cambial tissue. As tangential division continues, the cells that come to lie toward the inner face of each cambial strip begin to enlarge, chiefly in a radial direction; then they mature gradually into *secondary xylem.* Repetition of this history results in the continued formation of additional secondary xylem elements between the outer face of the xylem mass and the inner face of the cambium. Occasional cells on the outer face of the cambium mature into *secondary phloem* elements, which lie, therefore, between the cambium and the inner face of a primary phloem group.

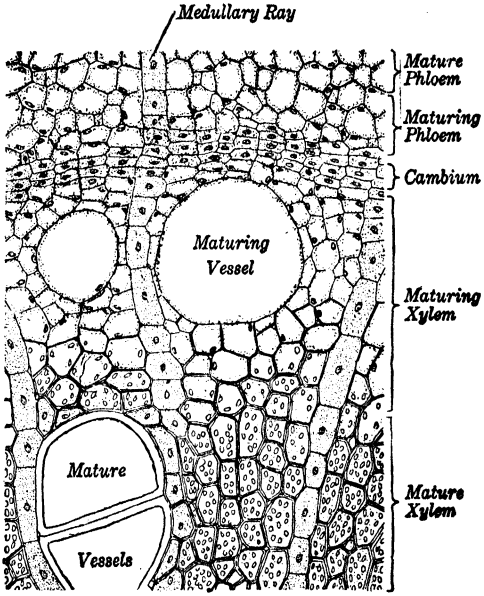


FIG. 24. Small portion of a cross section of a root of Ficus (the rubber plant), showing the formation of secondary phloem and secondary xylem by the cambium.

Shortly after cambial activity begins between the primary xylem and the primary phloem groups, some of the pericyclic cells just outside each ridge of primary xylem also begin to function as cambium. The cambium now forms a continuous sheath which completely surrounds the primary xylem (Fig. 23). In consequence of the method of their formation, the secondary xylem and the secondary phloem constitute two concentric cylinders that lie, respectively, within and without the cambium (Fig. 24). The cylinders of secondary xylem and secondary phloem are not continuous, because, at occa-

sional narrow regions in the cambium, cells are formed which remain thin-walled instead of developing into secondary xylem and secondary phloem. Such parenchymatous cells constitute strips (*medullary rays*) which run radially through secondary xylem and secondary phloem.

26. Secondary Tissues. The secondary xylem is variously organized in different plants. The roots of some plants contain a large proportion of water-conducting elements. In such roots these elements may consist of tracheids only, as in the pine; of vessels only, as in the willow; or, as in the oak, of both tracheids and vessels. In the roots of other plants the greater portion of the secondary xylem is composed of elements other than tracheids or vessels. Such elements, not primarily concerned in conduction, may be thick-walled (*mechanical*) elements which contribute to the efficiency of the root as an organ that anchors and supports the stem; or they may be parenchymatous cells which store reserve foods.

While they are very young the elements of secondary xylem and secondary phloem are arranged in definite radial rows in consequence of the method of their formation by repeated tangential divisions of the cambial cells. In such plants as the pine, whose secondary elements do not enlarge greatly during maturation, this radial arrangement persists. On the other hand, in many roots, such as those of the sunflower, vessels enlarge greatly while other elements of the secondary xylem remain small; consequently, in the mature secondary xylem the various elements are irregularly disposed, although some indication still remains of the original radial arrangement.

27. Annual Rings. In the roots of trees and shrubs, which live for several or many years, the formation of new secondary xylem and phloem continues from year to year. However, the xylem elements formed at the beginning of each season of growth commonly differ greatly from those formed later in the season. In the willow, for example, the vessels matured early in the spring are large and relatively thin-walled. As the season advances the successively formed vessels do not develop to so large a size, but their walls become thicker. The vessels produced toward the close of the growing season are smallest and thickest-walled of all. In late summer or early fall the formation of vessels by the cambium ceases. When, in the following spring, the cambium again begins

to form new secondary xylem, the first vessels matured are large and thin-walled. Consequently, a cross section of the root shows a sharp line of demarcation between the small-celled, thick-walled xylem of the preceding summer and the large-celled, thin-walled xylem of the spring. This is the explanation of the occurrence of concentric *annual rings* (Fig. 25), which are so conspicuous in the cut ends of roots of many trees and shrubs.

There are similar, though less sharply marked, differences between secondary phloem elements formed at the beginning, and those formed toward the end, of the growing season. Any annual ring of phloem does not, however, long remain intact, since the constantly enlarging cylinder of xylem and phloem within crushes it against the encircling tissues.

28. Cork Cambium. In the roots of many plants which form secondary xylem and phloem there are pericyclic cells that have retained the power of division. The tangential division of these cells results in the establishment of another cylindrical sheet of cambium (*cork cambium*, Fig. 26) which, instead of phloem and xylem, produces *cork cells* on its outer face and parenchymatous cells on its inner face. The walls of cork cells become impregnated with a fat-like substance; consequently the layer of cork so formed

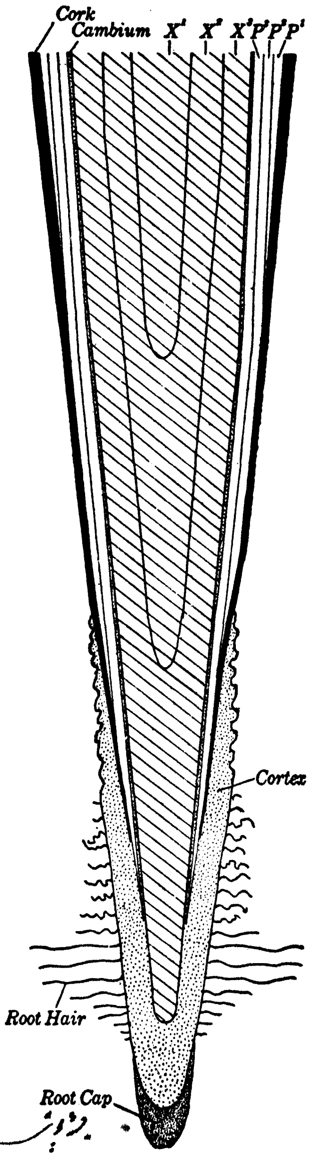


FIG. 25. Diagram of a root in lengthwise section, showing the relations of the annual rings of xylem and phloem. X^1, xylem (primary and secondary) formed during the first year. X^2, X^3, xylem formed during the second and third years. P^1, phloem formed during the first year. P^2, P^3, phloem formed during the second and third years.

deep within the root—that is, just inside the endodermis—is impermeable to water and to dissolved food substances. As a result, the cortical and epidermal cells outside the cork layer die and are eventually sloughed off. Thus, excepting for some plants whose roots form a cork cambium in their cortex, the mature portions of a root are derived entirely from the stele.

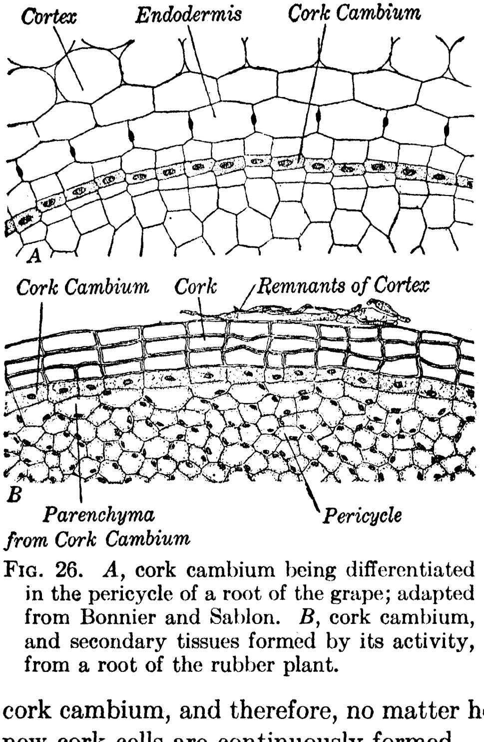


FIG. 26. *A*, cork cambium being differentiated in the pericycle of a root of the grape; adapted from Bonnier and Sablon. *B*, cork cambium, and secondary tissues formed by its activity, from a root of the rubber plant.

The cork cambium just described ordinarily forms new cork cells for a few years only and then becomes inactive. It does not follow, however, that no more cork is formed in the root; for additional cork cambium layers are successively developed in parenchymatous cells of pericycle and phloem inward from the original cork cambium, and therefore, no matter how old the root becomes, new cork cells are continuously formed.

29. Secondary Roots. It has already been said that branch or secondary roots may arise from a primary root. The development of such a secondary root begins with the division of certain pericyclic cells of the primary root adjacent to the group of tracheids in one ridge of primary xylem. As a result of these and of successive similar divisions, a small lens-shaped mass of embryonic tissue is formed. The outermost cells of this mass develop into a root cap; the innermost cells form the embryonic region of the secondary root. The secondary root grows through the cortex of the primary root to the surface (Fig. 27) and then pushes through the soil precisely as did the parent root. In penetrating the cortex of the primary root a young secondary root does not necessarily push aside the cortical cells; it may secrete substances that render

the materials of these cells soluble, the secondary root then growing into the cavity formed by their dissolution. Early in the development of a secondary root, the cells in the anterior and posterior portions of its embryonic region begin to undergo the processes of elongation and maturation already described. The various tissues matured in the secondary root are continuous with corresponding tissues of the parent root. Hence water and dis-

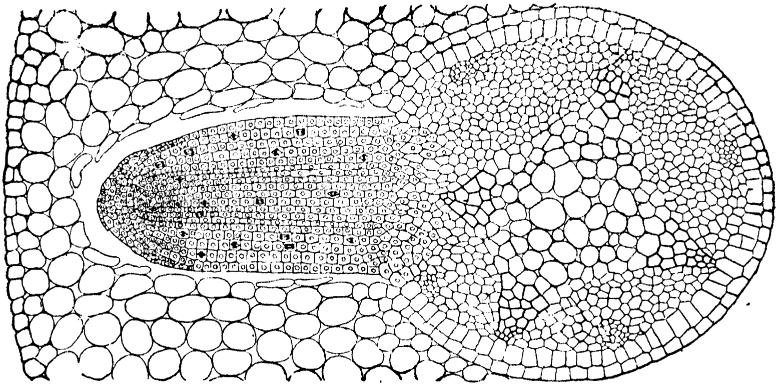


FIG. 27. Cross section of part of a primary root of the sunflower, showing the origin of a secondary root from the pericycle and its growth through the cortex of the primary root.

solved mineral salts can pass through the xylem of the secondary root to the xylem of the primary root and thence into the stem. Conversely, manufactured foods entering the phloem of the primary root may pass into the phloem of secondary roots. In plants whose primary roots undergo secondary thickening, each secondary root also may develop a cambium. Secondary phloem and secondary xylem, like primary phloem and primary xylem, are continuous from secondary root to primary root.

Since the development of secondary roots begins adjacent to the groups of tracheids in the ridges of primary xylem, secondary roots are formed in more or less definite rows, the number of rows usually corresponding to the number of ridges. For example, in the sunflower 3, 4, or 5 rows of secondary roots are formed at some distance back from the tip of the primary root, in its recently matured portion. Secondary roots usually begin to develop before the cambium has become a complete cylinder; if they develop after it has become continuous, the secondary roots originate in

the cambium rather than in the pericycle. Secondary roots so formed are not in regular vertical rows.

A secondary root, in the same manner as a primary root, may produce branch roots. The repeated formation of new branch roots, together with the growth in length of roots already formed, results in a continuous extension of the root system through the soil. The increase in number of roots, each bearing root hairs, increases the absorptive surface of the root system; the heightened water-absorption meets the growing need of the plant for water which results from the continuous enlargement of the aërial portion of the plant.

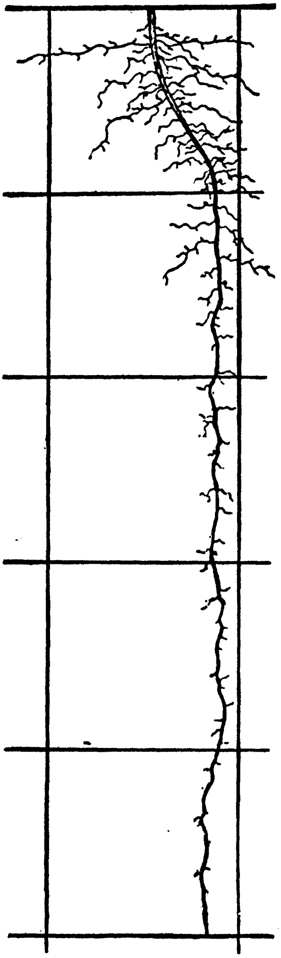


Fig. 28. The tap root system of alfalfa. After Weaver.

30. Types of Root Systems. It is a familiar fact that the aërial portion of a plant of a given species usually assumes a characteristic form. The root system of a plant of any species likewise commonly takes on a typical form. Some plants, including the corn and the pine, have relatively shallow root systems in proportion to the height of the stem; other plants, as the dandelion and the alfalfa, have comparatively deep root systems. It is to be remembered, however, that environmental conditions, especially the nature of the soil and the amount of moisture in the soil, profoundly affect both the shape and the extent to which a root system develops. For example, two-months-old alfalfa plants grown in a prairie region of the Missouri Valley had roots extending but a foot and a half below the surface of the soil; whereas plants from the same lot of seed and of the same age grown in more arid grasslands to the west developed roots extending to a depth of five feet.

Structurally, two main types of root systems are recognized:

tap root (Fig. 28) and *fibrous root systems* (Fig. 29). In a system of the former type, the primary root grows much more rapidly than any of the branch roots; the primary root then constitutes a central axis from which small branch roots arise. Sometimes, as in the

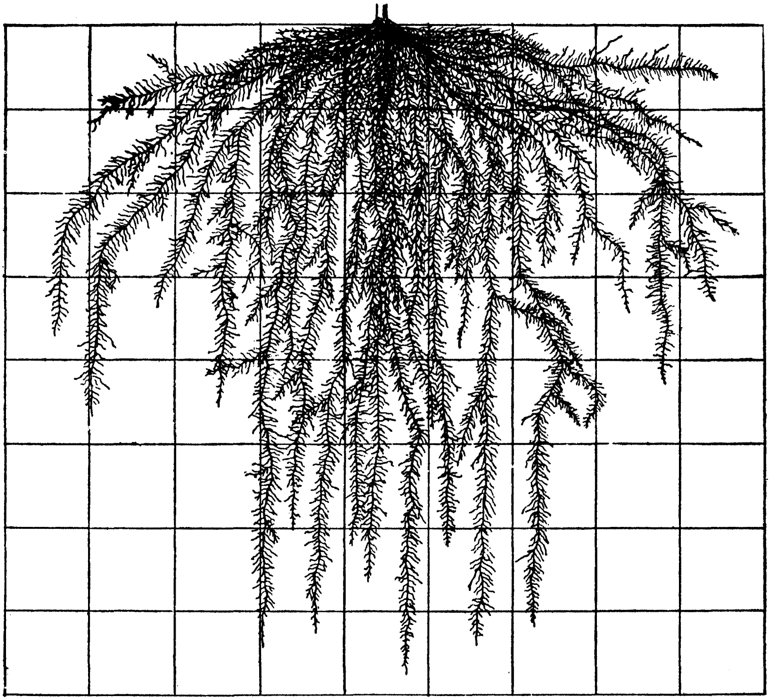


FIG. 29. The fibrous root system of corn. After Weaver.

pine, the primary root (a tap root) may die early. In such a case a secondary root takes on the appearance of a tap root. The tap roots of many plants attain a diameter approximately equal to that of the stem. This diameter is relatively small in plants that live but a year or less, but some trees, hickories for example, form thick, woody tap roots of large diameter and extending many feet downward. In some plants the diameter of the tap root may exceed by several times that of the stem. The great diameter of such a root is due chiefly to the formation of parenchymatous cells by the cambium; the cambium adding many such cells to the secondary phloem, as in the parsnip, or to the secondary xylem, as in the carrot and the radish. The economic importance of many

plants with fleshy tap roots results from the storage of large amounts of reserve starch in such parenchymatous cells.

A fibrous root system has no central axis. Instead, many of the secondary roots, and the primary root if it persists, grow to approximately the same length and diameter. Such a root system may be composed of relatively slender roots, as in the sunflower; or, if secondary thickening is long continued, various members of the root system may attain to a large diameter, as in most familiar trees. In the fibrous root systems of some plants, such as the dahlia (Fig. 30), some of the secondary roots become much swollen and enlarged for a part of their length and filled with food or water. The enlarged diameter of such a root is not usually the result of extensive secondary thickening, but is due rather to the enlargement of parenchymatous cells in the cortex or pith. Fibrous systems with such enlarged secondary roots are often termed *fascicled root systems*.

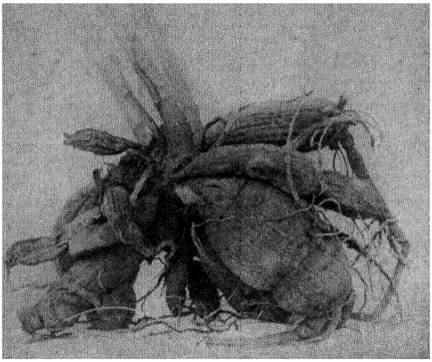


FIG. 30. Fascicled roots of the dahlia.

31. Adventitious Roots. Secondary roots may develop directly from stems and leaves much as they regularly develop from primary roots. Roots arising directly on stems and leaves are *adventitious roots*. Most plants with trailing or horizontal underground stems, such as the iris, most grasses, many ferns, and various vines, regularly produce numerous adventitious roots on their stems. Some plants with erect stems, like the corn, also regularly form adventitious roots.

Adventitious roots may supplement the work of primary and branch roots in absorbing water and food materials from the soil. In some plants, such as the corn and certain other cereal grains, the primary root and its branches may entirely disappear, all intake of water then being through the fibrous system of adventitious roots. Adventitious roots may function also as supports that help to hold erect the stem or its branches. Instances of this sort

are seen in the corn (Fig. 4), whose "prop roots" grow downward from the lower nodes of the stem into the soil; or in the banyan tree of India (Fig. 31), whose adventitious roots grow directly downward from horizontal branches to the soil. Some climbing plants, including the English ivy, develop many short adventitious

FIG. 31. A banyan tree, with many vertical adventitious roots. After Baillon.

roots along their internodes that aid the plants in clinging to their supports.

Many plants that do not regularly form adventitious roots do so under special conditions. When the tip of a raspberry stem bends over and touches the ground, the terminal portion in contact with the soil forms adventitious roots. Stems and branches of other plants, including the rose, geranium, and Coleus (Fig. 32), ordinarily form adventitious roots only when a stem or branch has been severed from the root system and placed in damp soil.

The common practice of propagating plants by cutting a stem or branch into segments is based upon the ability of such pieces (*cuttings*) to form adventitious roots when placed under appropriate conditions. This practice makes it possible to obtain a large number of new individuals of some species, such as the potato, that rarely form seeds. Propagation by cuttings also has the great advantage that it almost always results in the production of new plants precisely like the parent. In this way some especially

desirable strawberry, raspberry, or rose plant which, because of its hybrid nature, will not breed true by means of seeds, may be indefinitely multiplied.

32. Environment of Roots: The Soil. The soil is of importance to a plant in three main respects: it affords a dense medium in

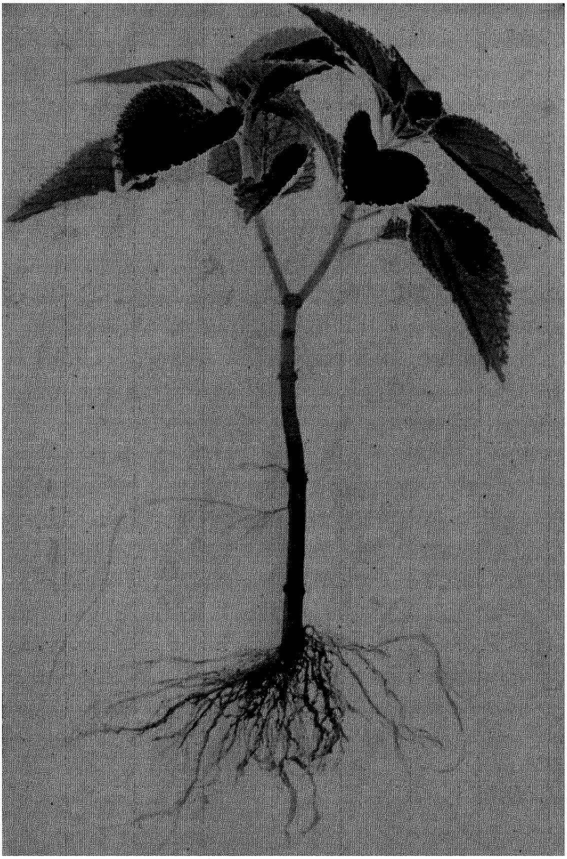


FIG. 32. Adventitious roots of Coleus, formed from the stem of a cutting placed in the soil.

which the plant is firmly anchored and supported; it is the source of a supply of water; and from it the plant takes in certain substances essential to its growth and development. The soil also provides a protective environment, during periods unfavorable for growth, for roots and other underground structures.

Although soils are exceedingly variable, most of them contain rock particles, humus, water, substances dissolved in water, air, and microörganisms. The particles which constitute the bulk of the soil have been formed chiefly from rocks by various disintegrating agencies such as glacial movements, frost, rain and running water, gases of the air, and winds. Some simple plants, including blue-green algae and lichens, by their gradual penetration of rocks aid in the process of disintegration. Such plants obtain needed mineral substances from the dissolved portions of the rocks upon which they grow. After the death of these plants their decaying bodies together with the mineral substances they have absorbed are returned to the soil. Further organic substances are added by the decay of the bodies of other and larger plants which may follow, and by the decay of animal bodies and of animal excreta. Thus organic matter accumulates in the soil. Through the agency of minute organisms the organic matter is constantly undergoing change, in the course of which it is transformed into simpler compounds. When the organic matter reaches a certain stage of decomposition it is called *humus*.

Humus, by separating the soil particles, increases the space which may be occupied by air; the physical texture of the soil is thus made more favorable to the growth of plants. Humus readily absorbs and holds water, so increasing the water-holding capacity of the soil. Although humus may remain in the soil for some time, it is finally completely decomposed into simpler compounds. While present it is the seat of an abundant and flourishing growth of minute organisms, many of which are of great importance to the nutrition of green plants. Certain animals, such as rodents, insects, and earthworms, also modify the physical condition of the soil.

Rock particles in the soil vary greatly in size. Soil materials may be classified on the basis of the size of their included rock particles as coarse gravel, fine gravel, coarse sand, fine sand, silt, fine silt, and clay. Clay, the commonest soil material, is found to some extent in soils of all classes. The smallest clay particles are too fine to be seen with a microscope. Although the small size and irregular shape of these particles enable many of them to fit together closely, nevertheless a considerable amount of space, occupied by air and water, is left between them. Sand, composed of larger particles, plays an important part in keeping the soil

open, but soils with a too high content of sand are infertile. The water-holding capacity of sandy soils is low; clays and silts hold water tenaciously. Soils containing both sand and clay are *loams*. Silt forms a considerable portion of loams. Loams may also contain humus, which is intermingled with the rock particles, and which further adds to the water-holding capacity of the soil. Soil particles may be held together by the films of water about them, or by substances such as clay which act as cements.

33. Functions of Roots. The functions of roots that have been already noted are: absorption of water and dissolved substances from the soil, anchorage and support of the stem, and storage of reserve foods. The roots of plants growing in unusual situations may function in still other ways. For example, the roots of many submerged water plants, as well as those of many swamp plants, are provided with large intercellular spaces which store the gases (chiefly carbon dioxide and oxygen) that are taken in by the plant or are given off by its cells. The roots of certain tropical plants that grow on rocks in swiftly running streams are flattened and blade-like and their cortical cells contain numerous chloroplasts. These roots function like leaves in the manufacture of foods.

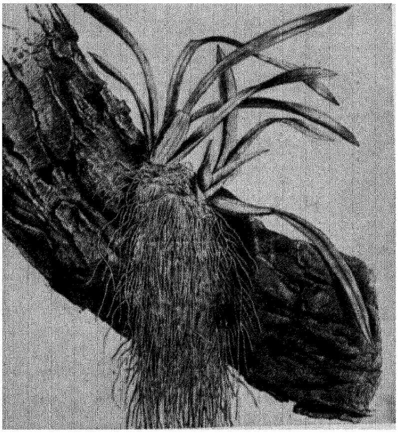


FIG. 33. Aërial roots of an orchid. After Kerner.

Other plants, including some tropical orchids (Fig. 33), growing high above the soil on stems and branches of other plants, bear roots many of which are exposed to the air. Each such aërial root usually has a spongy outer cell layer which holds and absorbs rain that falls or dew that condenses on its surface. Although the aërial roots may never penetrate the soil, they perform much the same absorptive functions as roots growing in the soil.

Summary

A root is divided into the following general regions: root cap, embryonic region, region of elongation, region of maturation, and mature region. The mature region consists of stele, cortex, and epidermis. The stele is composed of xylem (including tracheids and vessels), phloem (including sieve tubes), pericycle, and parenchyma. The cortex includes endodermis, parenchyma, and sometimes mechanical tissue. The epidermis is a single superficial layer of cells, many of which develop tubular projections (root hairs).

All the tissues thus far mentioned are primary since they result from the maturation of cells of the embryonic region. Some roots develop primary tissues only. Others develop secondary tissues as a result of cambial activity. The functioning of the cambium results in a formation of secondary phloem and secondary xylem, both interrupted by medullary rays. The secondary xylem produced in a single year's growth constitutes an annual ring. Cork cells and parenchyma formed by cork cambium are also secondary tissues.

Secondary roots developed from a primary root always have a deep-seated origin and arise in the pericycle. As they grow through the cortex they become differentiated into the parts characteristic of a primary root. Secondary roots developing directly from stems or leaves are adventitious roots.

The root system of a plant may be derived wholly from the primary root, or in part from the primary root and in part adventitiously, or wholly adventitiously. According to its external appearance it is a tap root system or a fibrous root system. Fibrous systems with enlarged secondary roots are fascicled root systems.

The functions of roots ordinarily include absorption of water and dissolved substances, anchorage and support of the stem, and storage of manufactured foods. Various special types of roots perform other functions.

CHAPTER V

STEMS

34. Regions of a Stem. As in the case of a root, the growing end of a stem includes an embryonic region, a region of elongation, a region of maturation, and a mature region. There are, however, certain differences. First, a stem has no structure corresponding to a root cap. Second, the transition from embryonic to mature region is not continuous in a stem as it is in a root, but is interrupted

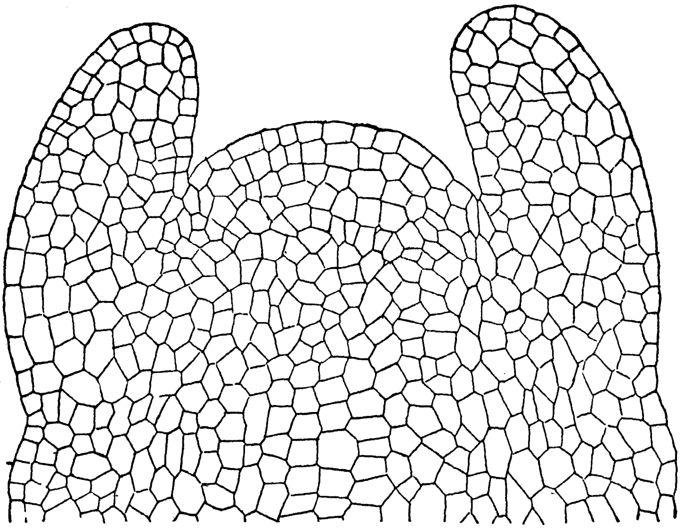


FIG. 34. Lengthwise section of the apex of the stem of a honeysuckle.

at intervals by the nodes, in which the processes of maturation lag. This lagging is especially noticeable in certain of the grasses, portions of whose nodes remain embryonic even after the internodal tissues are mature.

In the embryonic region at the apex of a stem (Fig. 34) and of each branch many of the cells are dividing. In this region the cells are all essentially alike. Along the sides of the embryonic region are small dome-shaped or spoon-shaped superficial outgrowths, each

composed of embryonic cells. These outgrowths (*leaf primordia*) are the beginnings of young leaves. The level at which one or more leaves are being formed is a node; the embryonic region of the stem is therefore beginning to be differentiated into nodes and internodes, but the internodes are as yet so short that successive nodes appear to adjoin one another (Fig. 35). As already noted, the enlargement and maturation of cells that follow are generally slower in the nodal than in the internodal portions of the stem.

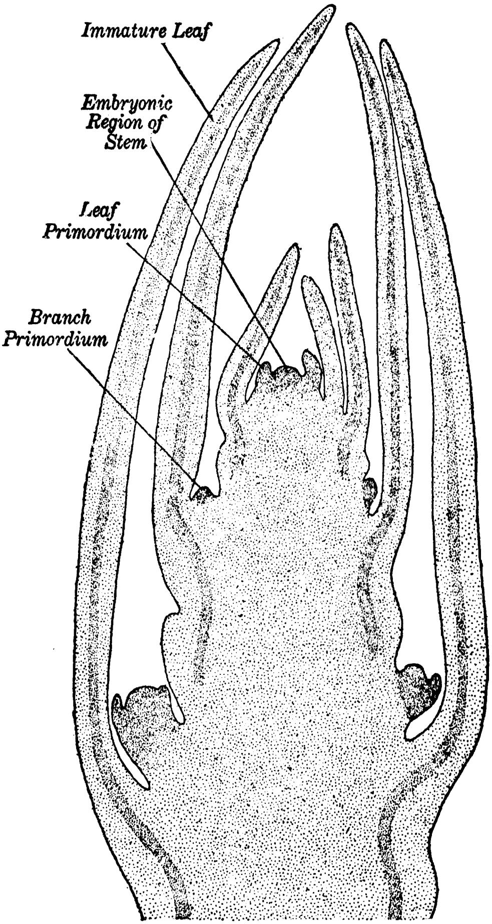


FIG. 35. Diagram of the apical portion of a honeysuckle stem.

In an actively growing stem elongation usually begins in the third or fourth internode from the stem's apex. The cells of such an internode are growing chiefly, though not exclusively, in length. Here, certain groups of cells which are to constitute the respective tissues in the mature part of the stem are becoming differentiated in size and shape.

Among the earliest cells to become differentiated in an elongating internode are those immediately beneath the epidermis. These cells enlarge somewhat and then deposit additional layers of wall material at their angles and on their outer and inner tangential walls. Such localized thickening of the walls results in the formation of a

mechanical tissue of considerable rigidity, whose chief function is to help hold the stem erect until other tissues are mature. After the stem is mature this mechanical tissue, though persistent, is of minor importance in the support of the stem.

In an elongating internode, at some distance inward from the surface of the stem, strands of cells are differentiated that extend vertically, and parallel with one another, through the internode. These strands, composed chiefly of elongated cells, will eventually mature into *vascular bundles.* They may therefore be spoken of as *provascular strands.* In gymnosperms and in most dicotyledons the provascular strands, as seen in cross section, constitute an interrupted ring. In most monocotyledons the provascular strands are numerous and scattered, although they also run vertically through each internode.

35. Primary Tissues of Dicotyledonous Internodes. Since the difference just noted is correlated with certain other differences between gymnosperms and dicotyledons on the one hand and monocotyledons on the other, it will be necessary to consider these two types of stems separately. The sunflower may be taken as typifying the usual arrangement of tissues in a dicotyledonous stem. The cells of the central part of the sunflower stem mature into large parenchymatous cells, the vertical length of each of which is about double its thickness. These parenchymatous cells constitute the *pith* (Fig. 36).

Just outside the pith is the region in which lie provascular strands. Beginning at the inner face of each provascular strand and progressing outward, the cells mature into *primary xylem.* Simultaneously, the cells constituting the outer portion of each strand mature, progressively from the outer face inward, into *primary phloem.* The portions of the strand maturing into xylem and phloem eventually approximate but never meet, because a narrow strip in the center of the strand remains embryonic and may later function as a *cambium.* A mature vascular bundle, therefore, consists of three main parts: the xylem on the inner side toward the pith, the phloem on the outer side, and the cambium between xylem and phloem. This side-by-side arrangement of phloem and xylem in vascular bundles is characteristic of the structure of stems, in contrast to the alternate arrangement of separate xylem and phloem bundles which characterizes the primary tissues of roots.

The most conspicuous elements in the primary xylem are vessels, comparable in every way with the vessels of roots. Primary

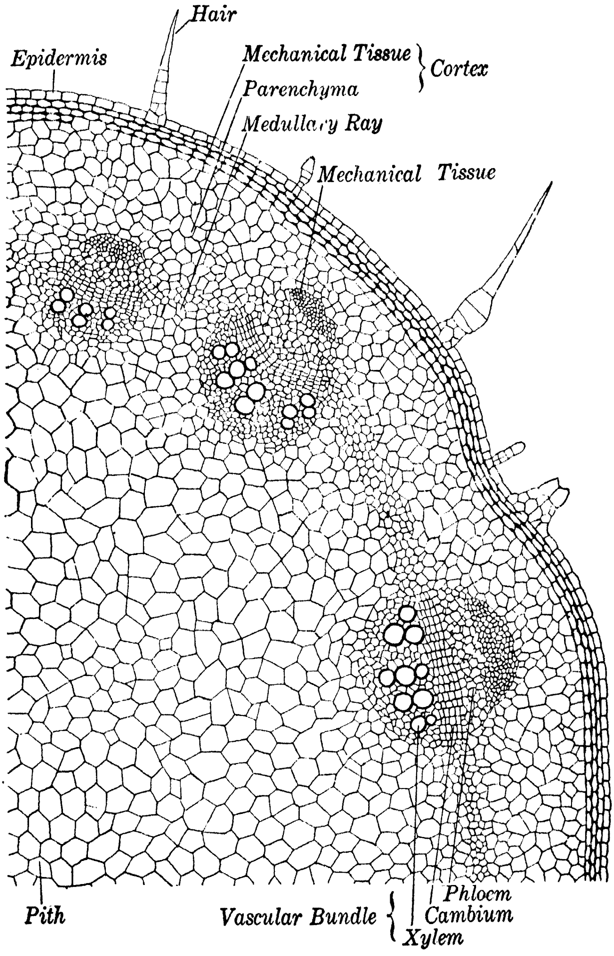


FIG. 36. Portion of a cross section of a sunflower stem.

phloem in stems, like that in roots, contains sieve tubes which are usually accompanied by companion cells.

The vascular bundles are separated from one another by radial strands of parenchymatous cells—the *medullary rays.* Surrounding the cylinder of bundles is a rather poorly delimited *pericycle.* Just

outside the phloem portion of each vascular bundle the pericycle consists of long needle-shaped cells whose walls, during maturation, are toughened and stiffened by substances with which they become impregnated. Since this change in the pericyclic cells does not take place until the internode is well along toward maturity, the *mechanical tissue* thus formed helps to hold erect only the mature portions of the stem. The pericyclic cells adjacent to the medullary rays are parenchymatous and scarcely distinguishable from ray and cortical cells. The pericycle constitutes the outermost portion of the *stele*.

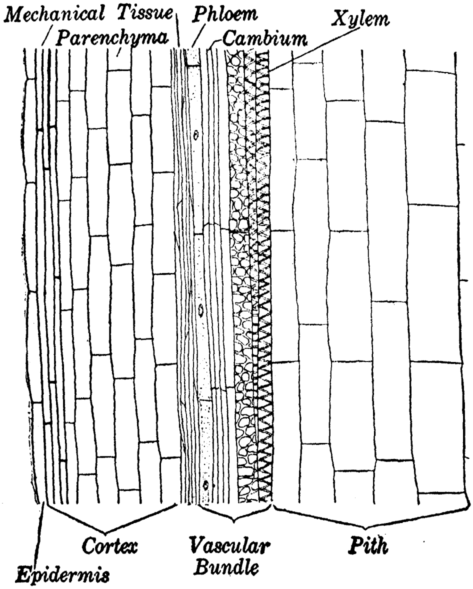


FIG. 37. Portion of a lengthwise section of a sunflower stem.

A relatively thin *cortex* surrounds the stele. In the sunflower the inner portion of the cortex consists of large, loosely arranged parenchymatous cells. An innermost endodermal layer is not differentiated. Stems and branches of some dicotyledons, especially certain horizontal underground branches like those of the potato, have an endodermis similar in structure to that of a root. As already mentioned, cells in the outer portion of the cortex with greatly thickened tangential walls constitute a mechanical tissue. These cells also contain many chloroplasts and manufacture a limited amount of food. All the cells of the cortex are elongated in the direction of the length of the stem (Fig. 37).

The cortex is bounded on its outer face by an *epidermis*. The epidermis is a single layer of slightly flattened, vertically elongated cells. Their outer walls are thickened and impregnated with a waxy substance (*cutin*), which makes the walls almost impermeable to water. Comparatively little water is lost, therefore, from the surface of a sunflower stem. Here and there an embryonic

epidermal cell matures into a long, pointed *hair*. Certain other epidermal cells develop into hairs, each composed of a row of several cells, the terminal cell being pointed. *Stomata* (which can be more satisfactorily studied in the leaf) also occur sparingly on the stem.

36. Structure of a Dicotyledonous Node. A very young node of a sunflower stem is a homogeneous mass of embryonic cells. One of the first changes as the node develops is the appearance of numerous provascular strands whose ends are continuous with the provascular strands of adjacent internodes. Although these strands are parallel, as has been seen, throughout each internode, they are laterally united with one another at various points in each node. In the mature stem, therefore, most of the vascular bundles of any internode are continuous with those of the internodes above and below; but in the nodes there are cross connections between the bundles.

In the cortical portion of each node of the sunflower stem three provascular strands are differentiated which run diagonally or almost horizontally through the cortex. Each such strand connects at its inner end with a provascular strand of the internode below and at its outer end with the base of an immature leaf. It follows that in the mature stem three of the bundles in each internode, instead of running vertically through the node above, bend outward in that node and run outward through the cortex to the base of a leaf. The portion of each such bundle that is developed in the cortex is a *leaf trace*. The leaf traces provide paths of transfer to the leaves for water and food materials that are moving up the stem and, conversely, paths of transfer to the food-conducting tissues of the stem for foods manufactured in the leaves.

Although seed plants in general have cortical leaf traces connecting their leaves with the vascular cylinder, the number of traces passing to each leaf varies in different species. For example, in tomatoes and carnations there is but one, in peppers there are five or seven, and in the buckwheat still more numerous traces connecting with each leaf.

37. Secondary Thickening in Dicotyledons and Gymnosperms. After primary xylem and primary phloem have been formed in the stem of a dicotyledon or of a gymnosperm, the cambial cells in the central part of each bundle begin to divide tangentially

As in a root, the new cells formed on the inner face of the cambium mature into secondary xylem elements and those formed toward the outer face mature into secondary phloem elements. The process of division extends to those layers of medullary ray cells which connect the cambial regions of adjacent bundles; the cambium thus in time becomes a continuous zone or cylinder (Fig. 36). The secondary xylem matured from the cambium now also constitutes a cylinder, continuous except where it is interrupted by medullary rays. Similarly, a cylinder of secondary phloem, continuous but for medullary rays, is formed outside the cambium. A few cells formed from the cambium remain thin-walled and are added to the medullary rays, so that these rays remain continuous parenchymatous layers connecting cortex and pith.

In the stem of a sunflower the cambium ordinarily produces secondary xylem and phloem for one season only, after which the stem dies. Many trees and shrubs have stems whose cambium, like that of their roots, continues the formation of xylem and phloem elements from year to year.

38. Structure of Secondary Phloem (Fig. 38). Secondary phloem may be simple or relatively complex in structure. In most gymnosperms the secondary phloem consists chiefly of sieve tubes on whose side and end walls are groups of pores; intermingled with the sieve tubes are a few parenchymatous cells. In the sieve tubes of a dicotyledon the groups of pores may occur in both end and side walls or in the end walls only. In the secondary, as in the primary, phloem of dicotyledons, a companion cell lies beside each segment of a sieve tube. The secondary phloem of dicotyledonous stems also includes parenchymatous cells, which are often densely filled with reserve foods. Vertically elongated cells (*bast fibers*), resembling, with their pointed ends and thick walls, the wood fibers of secondary xylem, occur in the secondary phloem of most woody dicotyledons and of some gymnosperms. In some woody stems, such as those of basswood and hickory, masses of bast fibers and of thin-walled elements (sieve tubes, companion cells, and phloem parenchyma) are formed alternately by the cambium.

Toward the end of the growing season, further functioning of the sieve tubes is usually prevented by the development of pads of additional wall material over each group of pores. During the next growing season the non-functioning sieve tubes with their

companion cells become crushed between the rigid "hard bark" outside and the expanding cylinder of newly formed secondary xylem and phloem within. Such parenchymatous cells and bast fibers as are included in the secondary phloem are more resistant

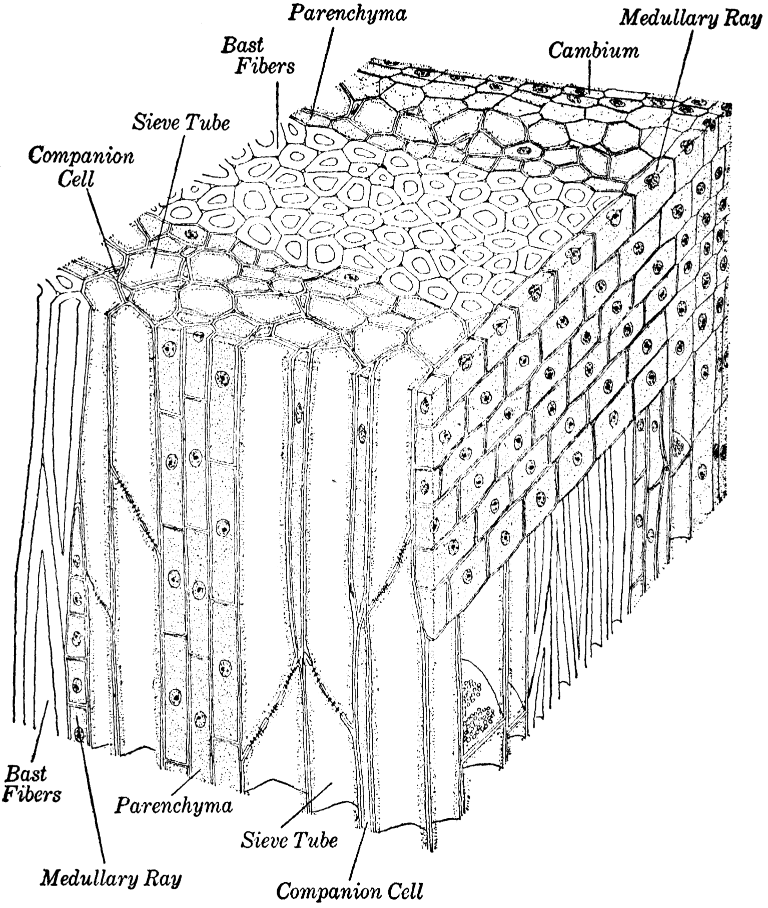


FIG. 38. Portion of the secondary phloem of a basswood stem.

to this crushing and usually persist in a more or less unmutilated state for several years.

39. Structure of Secondary Xylem (Fig. 39). The secondary xylem in the stems of gymnosperms, like that in their roots, consists chiefly of tracheids. Secondary xylem in stems of woody di-

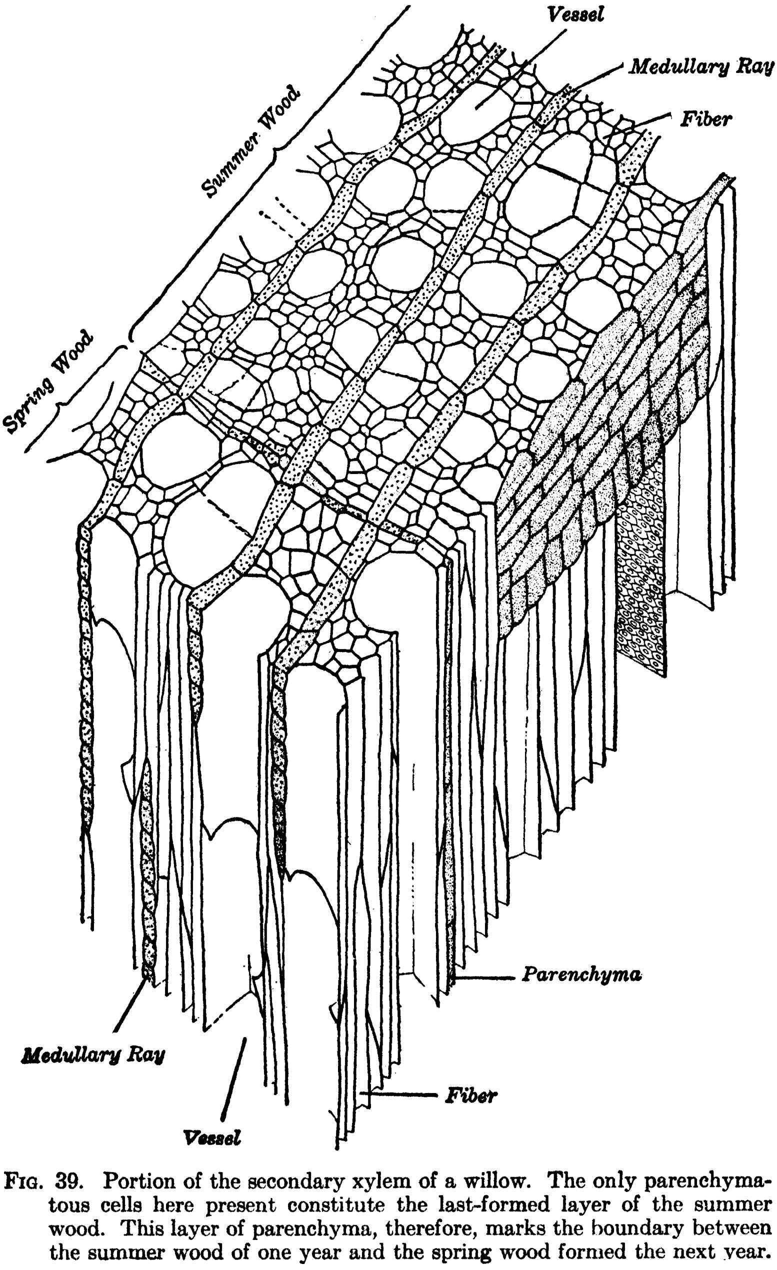


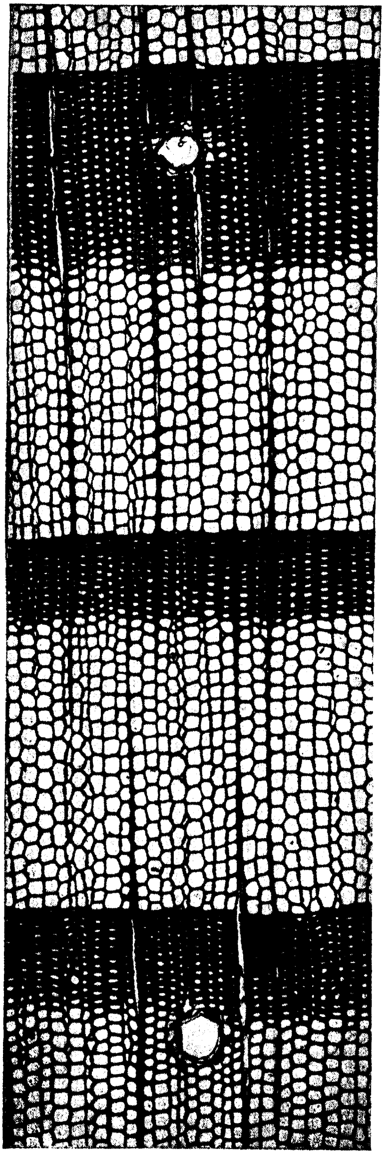
FIG. 39. Portion of the secondary xylem of a willow. The only parenchymatous cells here present constitute the last-formed layer of the summer wood. This layer of parenchyma, therefore, marks the boundary between the summer wood of one year and the spring wood formed the next year.

cotyledons, with a very few exceptions, contains vessels and may contain tracheids in addition. However, in stems these water-conducting elements constitute a smaller proportion of the secondary xylem than in roots. The remaining portion of the secondary xylem in stems consists largely of elongated, empty, pointed cells whose walls are strengthened and stiffened by substances with which they are infiltrated. Such *wood fibers* contribute to the rigidity of the stem. The secondary xylem of woody dicotyledons also contains parenchymatous cells. In some stems, such as those of the walnut and the hickory, parenchymatous cells are numerous in the secondary xylem; in other stems, as those of the willow and the cottonwood, only a few parenchymatous cells occur in the secondary xylem.

40. Medullary Rays. Each medullary ray in a sunflower stem is thick, that is, it consists of many layers of cells; it extends vertically from one internode to the next internode above. In most woody stems that increase in diameter for many years, such as those of the pine, willow, and apple, the rays are from one to five cells in thickness and from three to thirty cells in vertical height. In some woody dicotyledons, such as the oak and sycamore, certain rays are many cells in thickness and very many cells in height, whereas others are shorter vertically and but one to three cell layers in thickness. In all these woody stems, however, differently from the condition in the sunflower, the height of any ray is but a fraction of the length of the internode.

The secondary thickening of a woody stem is accompanied by the addition, through cambial activity, of new cells to the portions of the original rays imbedded in xylem and phloem. As the formation of secondary tissues continues, new rays originate from year to year at various points in the cambium. Such rays run radially, not through all the annual rings but only through some of the younger rings. Thus the number of rays increases from the inner rings outward, approximately in proportion to the increasing circumference of successively formed rings. The rays of a woody plant serve as a pathway for the lateral transfer of water, foods, and food materials between the inner and outer parts of the stem.

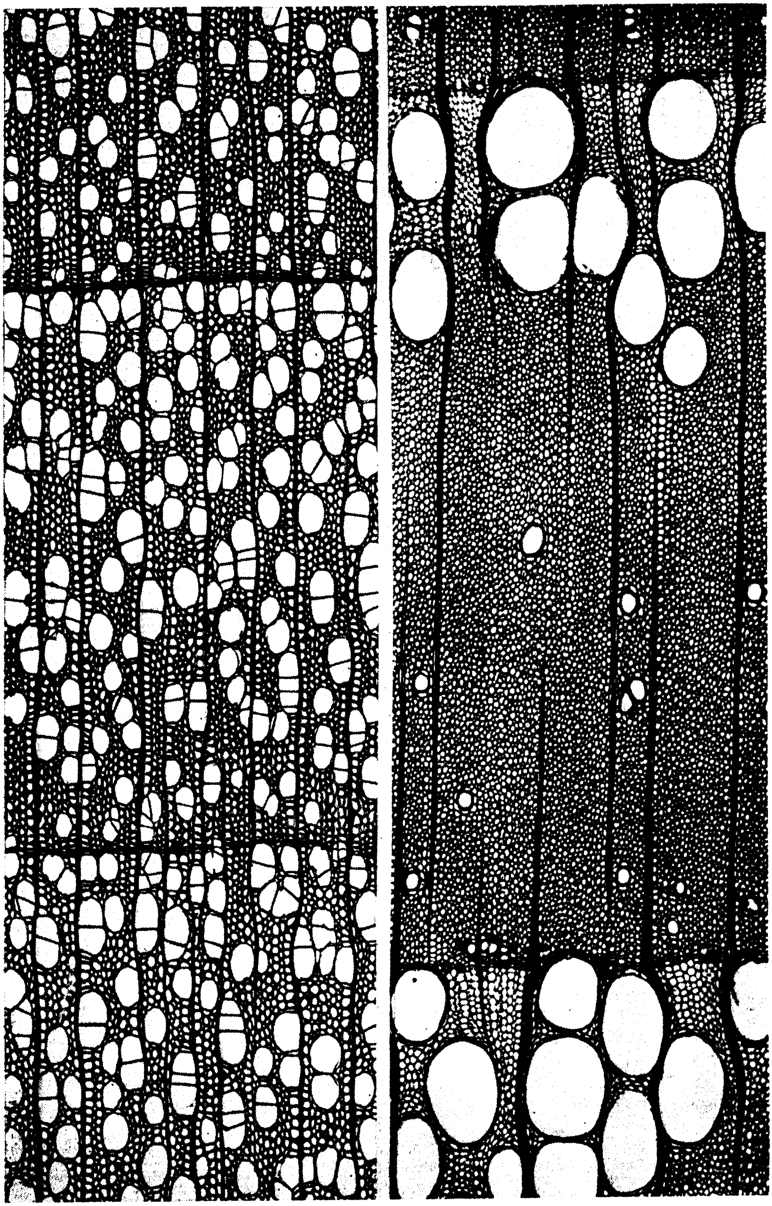
41. Annual Rings. The size differences between the secondary xylem elements produced at the beginning of each growing season (*spring wood*) and those produced later in the season (*summer*



wood) are even more noticeable in stems than in roots (Fig. 40). Such differences are especially characteristic of vessels, both in those species in which there is a gradual diminution in size of vessels from spring to summer wood (Fig. 41, *A*) and in those in which the transition is rather abrupt (Fig. 41, *B*). As a result of these differences in size of vessels, the annual rings in stems, especially of woody dicotyledons, are more sharply defined than are the annual rings in roots. Annual rings produced in successive years often vary greatly in thickness in consequence of variations in environmental conditions, especially in the supply of water to the plant. A permanent change in the environment, such as the felling of surrounding trees or the draining of a swamp in which a tree is growing, may result in marked differences in thickness between the annual rings produced before and those produced after the change (Fig. 42).

The number of rings in the xylem is not a perfectly accurate measure of the age of a tree, because sometimes, as a result of exceptional weather or other conditions, two rings are formed in

Fig. 40. Portion of a cross section through the secondary xylem of a trunk of the shortleaf pine. Two annual rings and parts of 2 others are shown. In this, as in other gymnosperm stems, no vessels are present. Photograph by the Forest Products Laboratory, Madison, Wis.



A *B*

FIG. 41. *A*, secondary xylem of the quaking aspen. *B*, secondary xylem of the black ash. Photographs by the Forest Products Laboratory, Madison, Wis.

a single year. In such a case the outer face of the inner or "false" ring is not sharply defined, but shows a gradual transition to the xylem formed later in the same season. Annual rings are sometimes much thicker in certain portions than in others. Differences of this nature may be brought about by a variety of conditions; they may result, for example, from a greater development either of roots or of branches on one side, as in a tree standing next to a clearing in a forest.

A

B

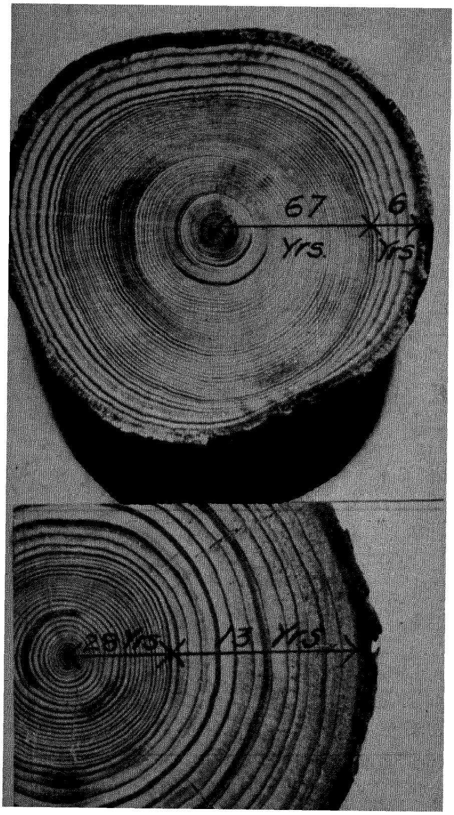


FIG. 42. *A*, cross section of a trunk of lodgepole pine, showing the greater width of annual rings produced after a thinning of the stand. *B*, cross section of a portion of a trunk of black spruce, showing the greater width of annual rings produced after draining the swamp in which the tree grew. Photographs by the Forest Products Laboratory, Madison, Wis.

42. Sapwood and Heartwood. As the number of annual rings in the wood increases, there comes a time when, in many stems, the vessels and tracheids of the inner rings become filled with gums and resins or blocked by bladder-like growths (Fig. 43) from neighboring parenchymatous cells of the xylem or of medullary rays. Such blocking of the water-conducting elements is usually followed by the death of all living cells in the annual ring, and frequently by an impregnation of the cell walls with dark-

colored substances. The xylem of the rings so modified becomes dry and is then known as *heartwood.* The sap (water and dissolved substances from the roots) must now travel upward in the outer, younger rings which constitute the *sapwood.* From year to year more rings in the inner part of the sapwood are changed to heartwood. Hence the sapwood of any particular tree remains of about the same thickness from year to year, whereas the heartwood is

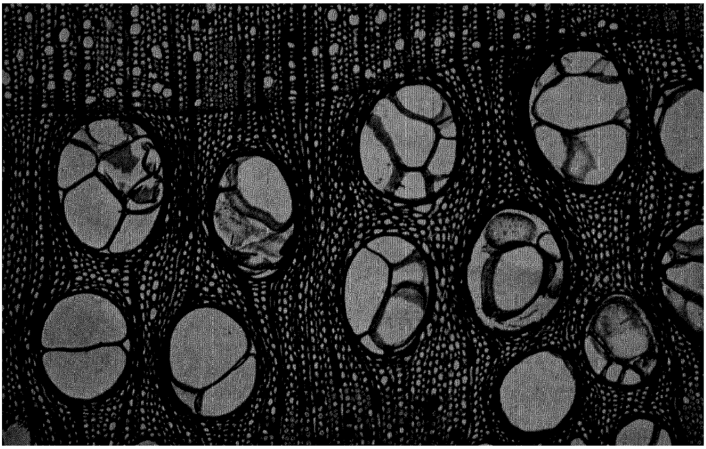


FIG. 43. Portion of a cross section through the heartwood of an oak. The vessels are filled by growths from neighboring cells. Photograph by the Forest Products Laboratory, Madison, Wis.

continually increasing in diameter. The sapwood may include only a few annual rings, as in the black locust or the black cherry, or, as in the hickory and the maple, it may be many rings in thickness. Xylem that has been changed to heartwood is often of greater mechanical strength than before the change. The development of heartwood in a tree may, therefore, increase the rigidity of the stem independently of any increase in the number of cells. It often happens that in very old trees the heartwood has decayed and disappeared, leaving the now hollow trunk composed almost wholly of sapwood.

43. Bark. The term *bark* is often used to designate all the tissues of woody stems from the phloem outward. The plane of separation, therefore, between wood and bark is the cambium. In a very

young branch or stem the bark is composed of phloem, pericycle, cortex, and epidermis. The stems of most trees and shrubs and of some herbaceous plants develop a *cork cambium* during their first growing season (Fig. 44). This cork cambium usually develops in the outermost portion of the cortex; but it may develop from the epidermis, as in the apple, or within the pericycle, as in the currant.

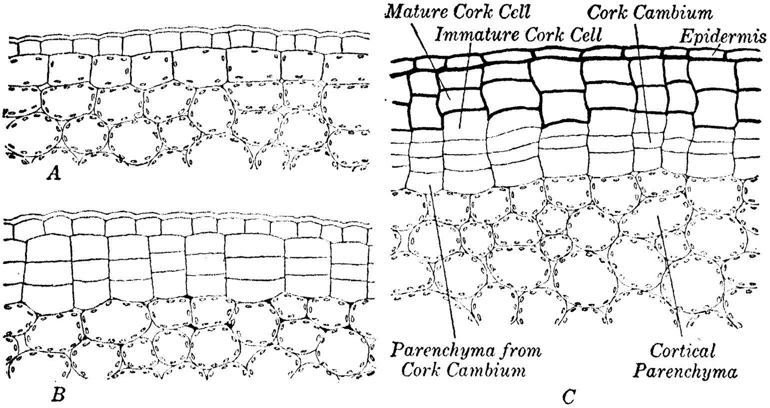


FIG. 44. Portions of cross sections of the outer region of a geranium (Pelargonium) stem. *A*, a young stem. *B*, the cork cambium beginning to function. *C*, the cork cambium has produced several layers of cork cells.

rant. The cork cambium of a stem, like that of a root, produces parenchymatous cells on its inner face and cork cells on its outer face. As in a root, the walls of the cork cells become impregnated with a fat-like substance which renders them impermeable to water; thus water is prevented from passing outward to the epidermal and cortical cells lying outside the cork layer; these outer cells die and their walls become dry and hard. Such outer dry tissues, together with the cork, are sometimes called "hard bark" in contrast to portions of the bark within the cork cambium, which are the "soft bark."

The cork at the inner face of the hard bark is usually but a few cells in thickness. In some plants, including the cork oak, which supplies the cork of commerce, many more layers of cork cells are formed, and the cork may attain a thickness of a half inch or more. In most perennial stems the original cork cambium becomes inactive after a few years; although this layer in some trees, such as the beech, cork oak, and some cherries, continues to form new

cork cells for many years. In woody plants whose first-formed cork cambium becomes inactive after a few years, additional cork cambiums are developed in parenchymatous tissues inward from the original cork cambium (Fig. 45). These newer cork cambiums appear successively in the inner portion of the cortex, in the pericycle, and in the outer layers of the phloem. Each successively

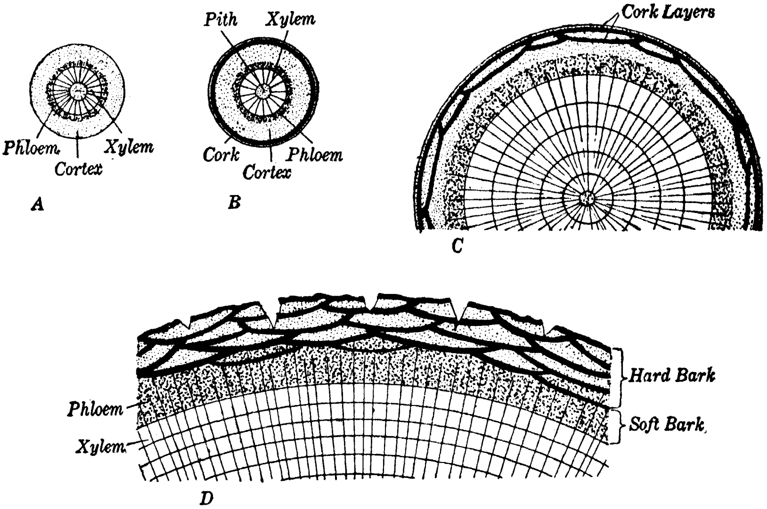


FIG. 45. Diagrams showing the development of cork layers and the resultant production of hard bark. *A*, before the differentiation of a cork cambium. *B*, the first cork cambium has produced a zone of cork (shown in black). *C*, later cork cambiums have developed and have produced strips of cork inside the original cork layer. *D*, an old stem with many cork strips, showing the cracking of the hard bark.

formed cork layer shuts off the supply of water and foods to such cells as lie outside it, the starved elements being added to the hard bark.

The cell layers constituting the hard bark often become cracked in consequence of the pressure of the expanding cylinder of xylem and phloem from within, and portions of the hard bark may become separated from the tissues within and fall away. The size and form of these separating portions of hard bark are influenced by the relative positions of successive cork cambiums, which are usually not continuous concentric zones but relatively short intersecting arcs. The manner and pattern of cracking of the hard bark are often distinctive of the species. Examples of characteristic

cracking are seen in the shaggy bark of hickories, the rough, deeply furrowed bark of oaks, and the shredded bark of grapes. Smooth

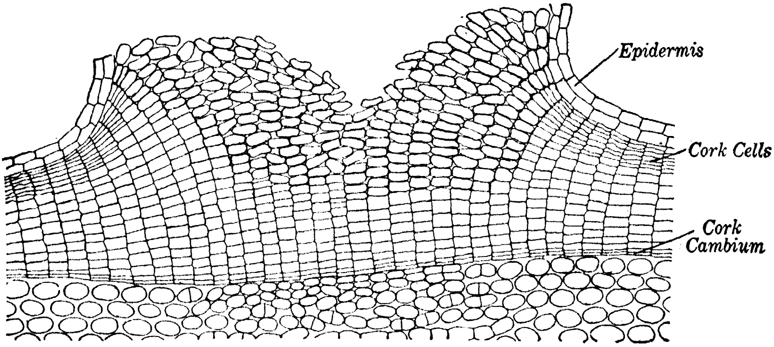


FIG. 46. Cross section of a lenticel of the elder.

bark, like that of a birch, is usually produced by the continued activity of the original cork cambium.

44. Lenticels. In the young portions of many stems certain limited regions of the cork cambium, usually beneath stomata, become particularly active. Repeated tangential divisions in each such region produce a mass of cells, the pressure caused by whose enlargement ruptures the epidermis; the cellular mass then protrudes as a small rounded or elongated swelling called a *lenticel* (Fig. 46). The characteristic horizontal markings of birch (Fig. 47) and cherry stems, as well as the rounded markings on young twigs of the horse-chestnut, are lenticels. Between the cells of a lenticel are intercellular spaces continuous with those of the cortex, which make possible a free interchange of gases between the outer atmosphere and the interior of the stem.

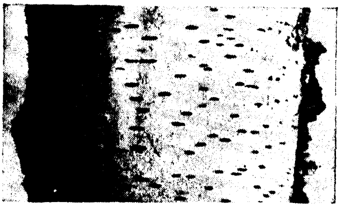


FIG. 47. Portion of a birch stem, with many horizontal lenticels.

45. Tissues of a Monocotyledonous Stem (Fig. 48). The stem of the corn may be taken as a typical monocotyledonous stem. While the young internodes are elongating, many scattered, parallel provascular strands appear in each. Later these strands mature into vascular bundles. The peripheral cells of each strand mature into long, thick-walled cells which constitute a mechanical tissue completely enclosing the bundle (Fig. 49). This sheath of mechani-

cal tissue is thickest on the inner and outer sides of the bundle. The remaining portion of the strand matures into primary xylem and primary phloem. As in the sunflower, there is a progressive maturation of phloem beginning at the outer face, and a progressive maturation of xylem beginning at the inner face, of each strand. Differently from the condition in the sunflower, matura-

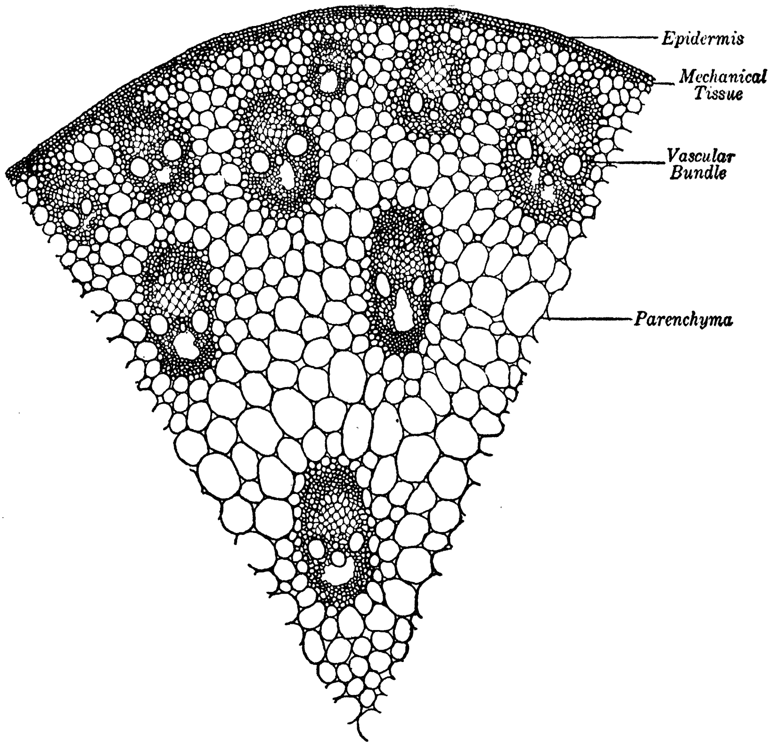


Fig. 48. Cross section of a portion of a corn stem.

tion continues until the whole strand (except the sheath of mechanical tissue) is converted into xylem and phloem. There is, therefore, no embryonic region (cambium) separating xylem and phloem, and no possibility of the formation of secondary elements between primary xylem and primary phloem. The phloem consists of regularly arranged sieve tubes and companion cells. The xylem of each mature bundle includes two large vessels with pitted walls adjacent to the phloem, and between these vessels a few

tracheids. The innermost portion of the xylem contains one or two vessels whose walls have spiral or ring-shaped thickenings. Just outside the latter vessel or vessels is a large intercellular space

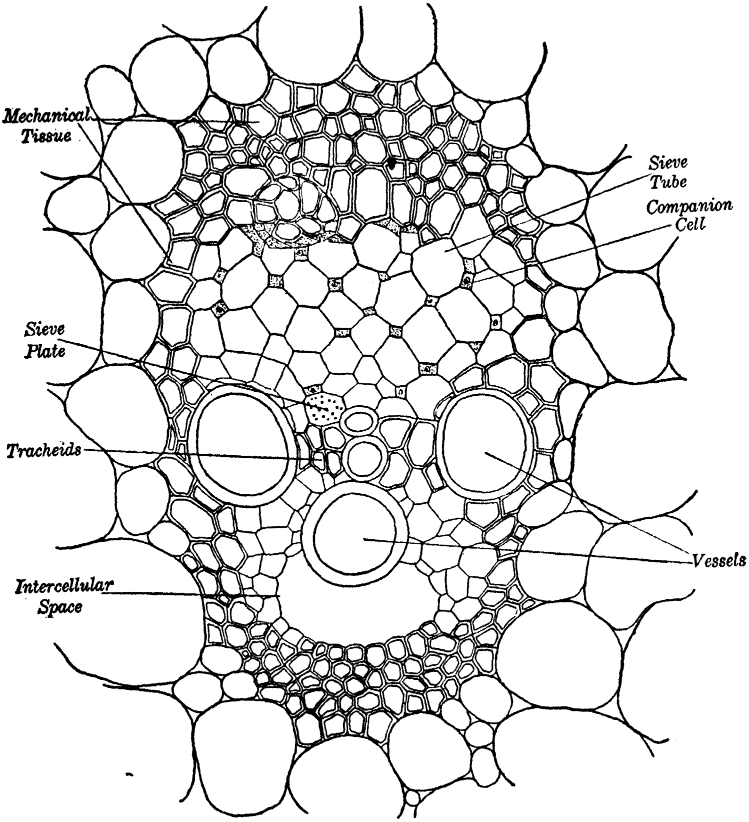


FIG. 49. A vascular bundle from a corn ste[illegible]

that separates this region of the xylem from the she[illegible] mechanical tissue.

The greater part of the stem consists of large p[illegible]ymatous cells. Scattered throughout this tissue are vascula[illegible]les. The parenchymatous cells in the central part of the ste[illegible] be compared with the pith, and those in the peripheral p[illegible]with the cortex, of the sunflower. It is impossible, however,[illegible]tinguish sharply in the corn stem between pith and cortex[illegible]side the parenchymatous tissue is a narrow cylinder of me[illegible]l tissue,

most of whose cells are small and thick-walled. Outside this is an epidermis of relatively small, thick-walled cells.

Since the corn lacks a cambium, its stem can not increase in diameter after all the primary tissues are mature. The absence of a cambium is the chief feature distinguishing most monocotyledonous stems from stems of gymnosperms and dicotyledons. Other respects in which monocotyledons differ from the majority of di-

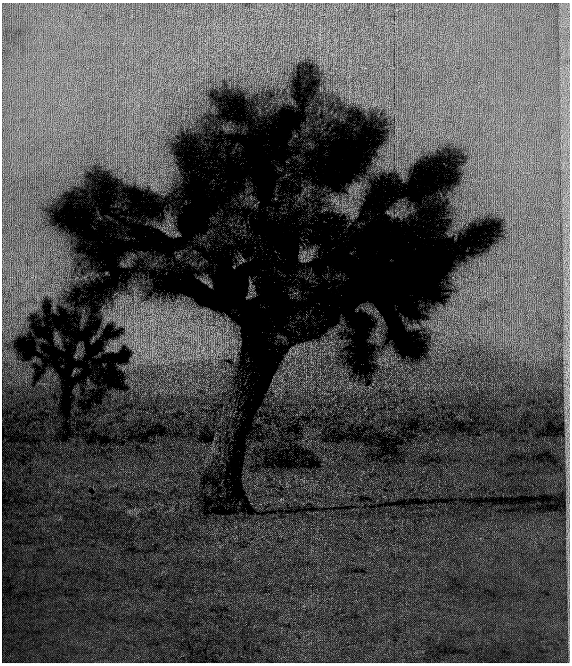


FIG. 50. The Joshua tree (*Yucca arborescens*), a monocotyledonous tree of the Mojave Desert. Photograph by Forrest Shreve.

cotyledons and from gymnosperms are the scattered arrangement of the vascular bundles, the presence of a sheath of mechanical tissue partially or completely surrounding each vascular bundle, the lack of a well-defined cortex, and the lack of medullary rays.

46. Growth in Thickness of Monocotyledonous Stems. The stems of most monocotyledons, since they contain no cambium, are incapable of growth in thickness after the cells in any particular

region have attained their full size. Hence certain monocotyledons, such as some bamboos, although they grow to a considerable height, remain slender. The trunks of some other monocotyledons, like the date and the coconut palm, taper gradually from base to apex. In such a case there is a progressive enlargement and maturation of cells from the apex of the stem to the base. The greater diameter of the basal portion of the trunk is due, therefore, not to the formation of new cells but to the delayed enlargement of the cells which were formed when that region was embryonic.

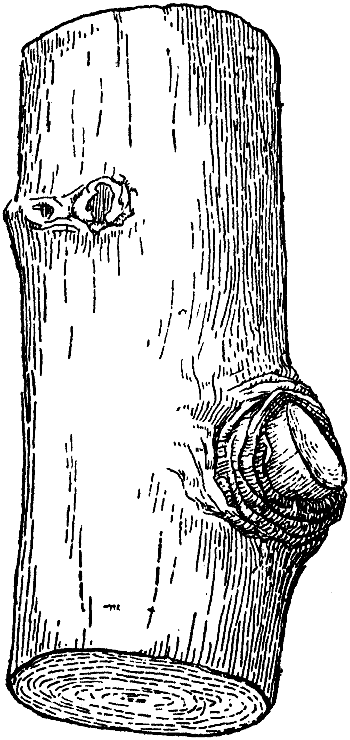


FIG. 51. Growth of wound tissue about the base of an amputated apple branch.

The stems of a few monocotyledons, such as Yucca (among whose species are the Joshua tree of the Southwest, Fig. 50), Aloe, and Dracaena (the dragon tree), undergo a true secondary thickening, although their vascular bundles are without cambium. In Dracaena, a cylinder of embryonic cells in the pericycle functions as a cambium, by whose means the stem grows slowly in thickness from year to year. Groups of new cells formed on the inner side of this cambium develop into vascular bundles; the new cells formed on the outer side of the cambium remain parenchymatous. A famous dragon tree of the Island of Teneriffe attained a height of approximately 70 feet and a circumference of 45 feet.

47. Wound Tissue. An important distinction between embryonic and mature cells consists in the power of division of embryonic cells. This distinction is, however, a relative one, since under unusual stimuli many apparently mature cells divide. One stimulus which so affects mature cells is that supplied by a wound. When a branch is cut from a stem, cell divisions begin in such parenchymatous

tissues as lie immediately adjacent to the cut surface, especially in those of the cambium and the soft bark. The result is the formation of a *wound tissue* or *callus* (Fig. 51). The walls of the outer cells of the callus become impregnated with waxy compounds and function in the same manner as walls of cork cells. Certain deeper-lying callus cells become a cambium which is continuous with the cambium in the stem. The cambium developed within the callus forms secondary xylem and secondary phloem in the usual manner, and the resultant tissues, together with such callus cells as lie external to them, gradually grow over

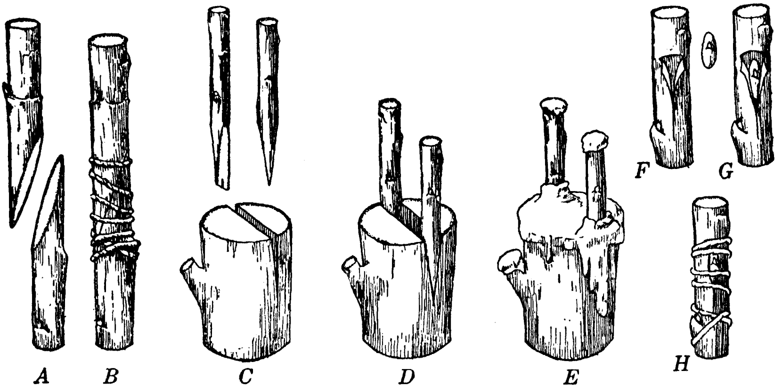


FIG. 52. Methods of grafting. *A*, *B*, between stock and scion of similar size. *C*, *D*, *E*, between a large stock and small scions. *F*, *G*, *H*, bud-grafting.

the xylem exposed by the wound. In time the callus may extend completely across the wounded surface, which, as additional elements are added, is more and more deeply buried. The healing or covering of exposed surfaces by a callus largely prevents the entrance into the wood of decay- and disease-producing organisms.

The formation of wound tissue on cut surfaces makes *grafting* possible. Grafting is commonly used in the propagation of such woody plants as do not readily form adventitious roots on cuttings. By this means it is possible to obtain new individuals of species which produce no seeds, such as seedless grapes or navel oranges, or to obtain duplicates of some desirable plant which, because of its hybrid nature, will not breed true by means of seeds. The two members of a graft are the *stock*, a root or the base of a stem with the attached root system, and the *scion*, a branch or bud which is

to grow into the fruit- or flower-bearing portion of the grafted plant.

Grafting (Fig. 52) may be between a stock and a scion of the same size, between a large stock and a small branch, or between a large stock and a bud. In all cases the success of the graft depends upon the close proximity of the cambiums of the two members, and upon the prevention of a drying of the united faces during the establishment of the graft. Grafts are usually established only when the two members are from plants of the same or of closely related species.

48. Structure of Wood. The great diversity among trees of different species in type, number, and distribution of component

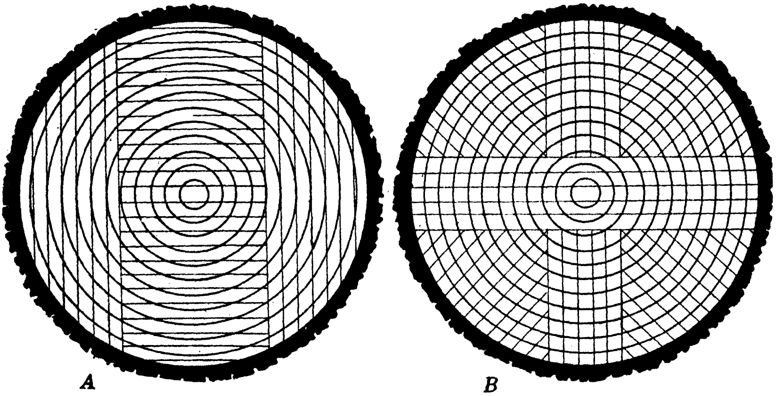
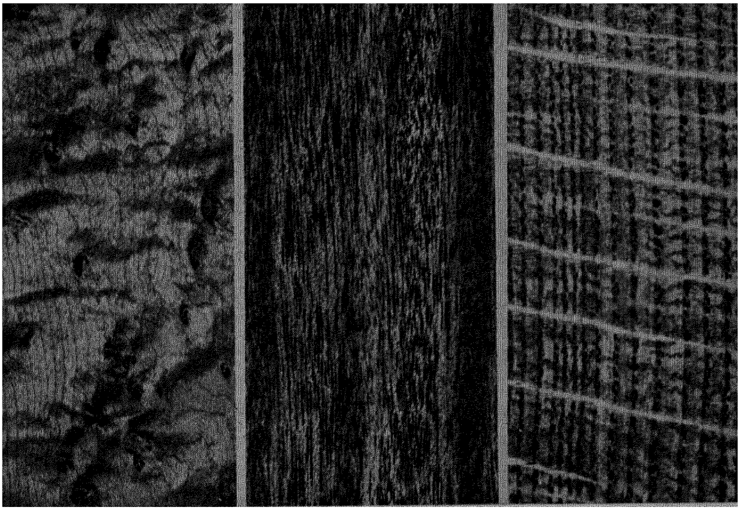


FIG. 53. Methods of sawing a log. *A*, plain sawing. *B*, quarter sawing.

elements, the variations in width of annual rings and in relative amounts of spring and summer wood, and differences in size of medullary rays, result in marked differences in strength, workability, texture, and surface pattern of their woods when used for building or other purposes. The presence of numerous thick-walled fibers in the xylem of the oak or of broad layers of thick-walled summer tracheids in the annual rings of southern yellow pine results in a timber that is most suitable for use where strength is especially required. Sharp differences between spring and summer wood, or the presence of masses of fibers, may, however, result in a timber that is hard to work and therefore less desirable than one which, like that of the white pine, has a uniform texture. Even when the secondary xylem of two species is composed of similar

elements and includes similar proportions of spring and summer wood, differences in the length of elements and in the nature of the cell walls may make the two sorts of timber markedly different in character. It is for such reasons that spruce is much tougher and lighter than most pines.

Woods differ markedly in color, in figure or grain, and in surface texture. Color is affected chiefly by changes incident to the transformation of sapwood into heartwood; the heartwood may be black as in ebony, brown as in walnut, or red as in mahogany. The



A *B* *C*

FIG. 54. *A*, plain-sawn bird's-eye maple. *B*, ribbon effect of quarter sawing "Philippine mahogany." *C*, quarter-sawn oak. Photographs by the Forest Products Laboratory, Madison, Wis.

patterns produced on an exposed surface by medullary rays, fibers, and other elements, as well as by the alternations of summer and spring wood, make lumber cut from certain species especially valuable for furniture and for the interior finish of buildings. The pattern depends largely upon the manner in which the lumber is sawn from the log. There are two general methods of sawing logs (Fig. 53): "plain sawing," the lumber being cut at right angles to the medullary rays; and "quarter sawing," the cutting being parallel to the rays. Plain sawing is especially desirable in logs with contrasting cylinders of spring and summer wood, such as

those of southern yellow pine, cypress, and redwood, or with elevations or depressions in the cylinders of summer wood. Plain sawing of this latter type of log, as in curly and bird's-eye maple (Fig. 54, *A*), produces a pattern of circular and wavy summer-wood lines against a background of spring wood. Quarter sawing, on the other hand, may give a surface with a more striking pattern than does plain sawing (Fig. 54, *B*, *C*). In oaks and sycamores this pattern results largely from contrasts in color between medullary rays and other elements. Quarter sawing of maples, birches, and mahoganies gives a wavy surface view of the fiber mass, or, as in some mahogany logs, a ribbon-like surface view of alternately inclined fiber masses in adjacent rings.

49. Branches. A branch begins as a small rounded hump of embryonic tissue in the axil (the angle between leaf and stem) of a young leaf just back of the embryonic region of the stem (Fig. 35). Although there is usually such a *branch primordium* in the axil of each leaf, only a few of the primordia ultimately develop into branches.

If the plant is one whose normal span of life is a single year, the primordia destined to become branches begin to elongate soon after they appear. Elongation is soon followed by an organization in each elongating primordium of regions corresponding to those present in the stem—namely, an embryonic region, a region of elongation, a region of maturation, and a mature region. The tissues matured in the branch are similar to those of the stem, and each tissue of a branch is continuous with the corresponding tissue of the stem. Water and food materials may therefore pass from the xylem of the stem to that of the branch, and foods manufactured in the branch may pass through its phloem to that of the stem. The secondary tissues of the branch are similarly continuous with those of the stem.

Branch primordia of most trees and shrubs do not develop into branches during the year that they appear, but, after developing to a certain stage, they remain dormant or continue to grow very slowly. Such *buds* may begin to elongate rapidly the year after they are formed, or they may remain dormant for several or many years.

The growth in length of a stem and of its branches is accompanied by the formation of an ever-increasing number of new branches. If all such branches were to persist and to increase in

diameter by secondary thickening, the system of branches might become so closely crowded that they with their leaves would densely shade one another. Such a condition is rarely found in trees, however, because many of the young branches die within a few years of their formation. In some trees, such as the cottonwood,

FIG. 55. A pine growing at a relatively high altitude (Sentinel Dome, Yosemite), showing the dwarfing and distorting effects of snow and wind. Photograph by Phillips D. Schneider.

the death of a branch is due to the development of a basal transverse tissue, an *abscission layer*, which causes the branch to become separated from the stem or older branch bearing it. In most trees no abscission layer is formed at the base of a branch; a dead branch remains attached to the tree until it is broken off by storms or by other means.

50. Kinds of Stems. Plants which develop tall, woody stems capable of standing erect without support are called *trees*. Each species of tree has, in general, a characteristic form. The trunk of the black spruce tapers gradually without forking from base to apex and produces whorls of branches, the branches of the older whorls being largest and those above progressively shorter. The outline of such a tree is that of a cone. Some other gymnosperms,

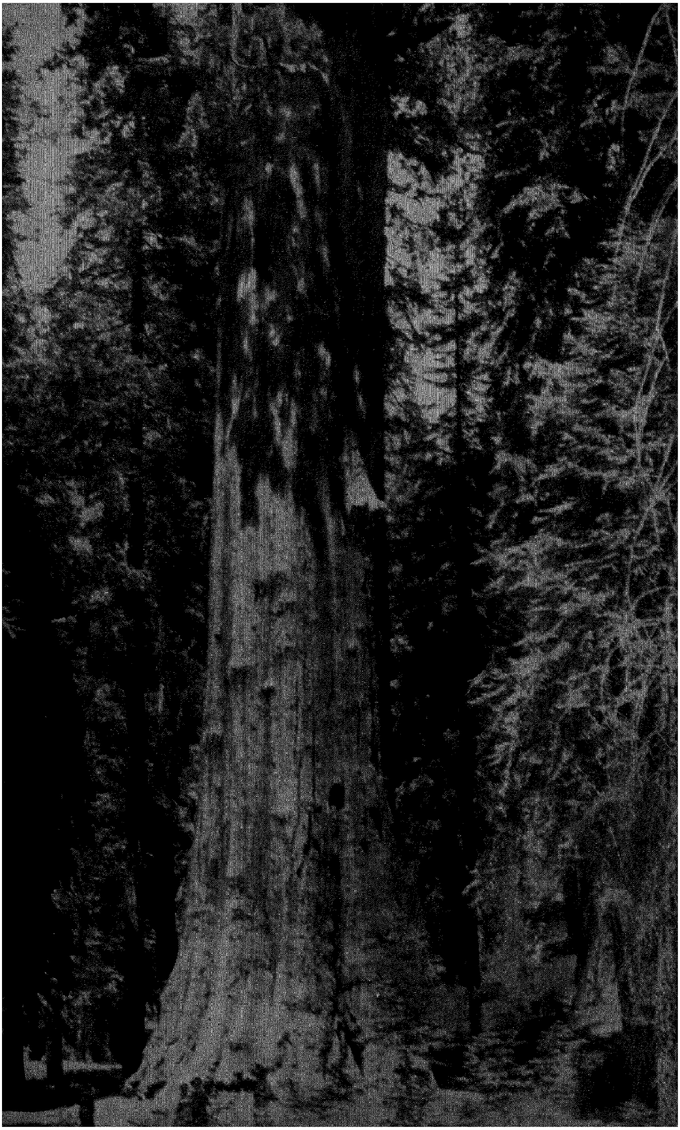


FIG. 56. One of the "big trees" of California. Photograph by Lenwood Abbott, from *American Forestry.*

such as the larch (Fig. 70), have a similar habit of growth. The form of such trees as the elm (Fig. 72) and the oak is usually very different from that of the spruce. At some distance above the ground there ceases to be a single trunk; instead, a varying number of large branches appear, which are themselves often much branched. Such a tree frequently has a rounded form (see also § 58).

The height of a tree and the thickness of its trunk vary with the species, with the age of the tree, and with the environment. At high elevations, plants of species which at lower levels develop into trees often have small, twisted, gnarled, and more or less prostrate stems (Fig. 55). Under conditions that favor growth, trees of certain species attain a great height and develop huge trunks. The "big trees" (*Sequoia gigantea*) of California are notable illustrations (Fig. 56). One of the largest of these trees is 325 feet in height, and the trunk, at a short distance above the ground, has a diameter of nearly 30 feet. The numbers of annual rings counted in the stumps of a few Sequoias indicate that the trees were over 3,000 years old when felled, the oldest one thus far counted having been somewhat more than 3,200 years of age.

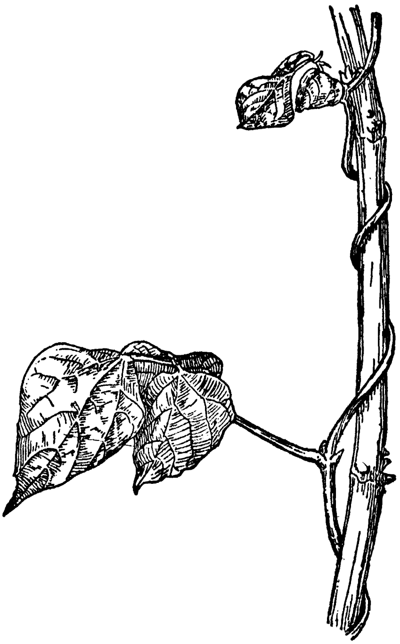


FIG. 57. The twining stem of a bean.

Plants which develop relatively short and usually freely branched woody stems are called *shrubs*. Since trees and shrubs intergrade, the words "shrub" and "tree" are convenient, but not exact, terms.

Those plants whose stems develop a small proportion of xylem, their stems therefore frequently remaining relatively soft, are called *herbs*. The distinction between herbaceous and woody plants is likewise not a sharp one, for almost all gradations in the amount of xylem developed may be found in different plants.

The stems of many plants can not hold themselves upright, either because of their slenderness or because of the small proportion of mechanical tissue. Some such weak-stemmed plants merely creep or clamber along the ground or over rocks. Others (often called *vines*) attach themselves to supporting objects, such as other plants, and so attain an approximately upright position. Clambering and climbing plants may be either woody or herbaceous. Some vines, such as the morning glory and the lima bean (Fig. 57), climb by means of a twining of their stems, the terminal portion of such a stem moving through a rather large spiral as a result of irregularities of growth on different sides. If a stem of this type comes in contact with a suitable support, the spiral movement of the terminal portion causes the stem to twine about the supporting object. The coils are at first often very loose, but later, through a straightening of the stem, the spirals become steep and firmly bound about the support. Other vines climb by means of tendrils. The tendrils of the garden pea (Fig. 76, *A*) correspond to leaflets; those of the grape (Fig. 58) to branches. Tendrils are usually sensitive to contact, especially toward their tips. Contact with an object serves as a stimulus, and, in the cases of most tendrils, the end within a short time becomes tightly wound about the object touched. In the Japanese ivy and the Virginia creeper, the small branches of the tendrils end in knobs. Upon contact these knobs broaden into disk-shaped structures that adhere with extreme tenacity to the surface with which they are in contact. Certain plants,

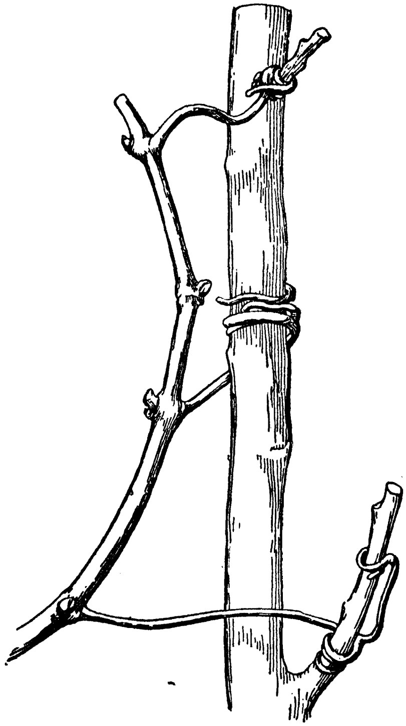


FIG. 58. Tendrils of the grape.

such as the English ivy, climb by means of adventitious aërial roots.

The stems of many plants grow underground. A whole stem with its branches may be underground, as is the case in many

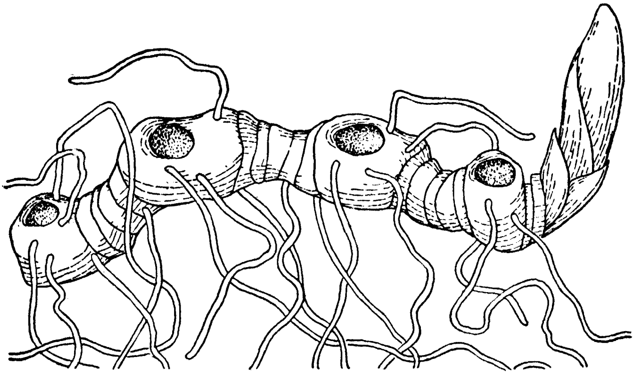


FIG. 59. Underground stem of Solomon's seal.

ferns; or, more frequently, the underground stem produces aërial branches which bear foliage leaves and flowers. The latter case is illustrated by cat-tails, sedges, grasses, and golden-rods. Underground stems (Figs. 59, 60) often contain a considerable amount of

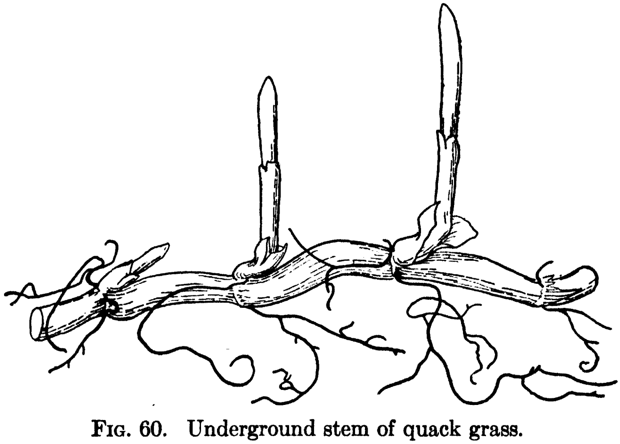


FIG. 60. Underground stem of quack grass.

food. If such a stem is broken into numerous parts, roots and aërial branches may be developed at each node, new plants thus being produced. It is for this reason that certain grasses, like the quack

grass, are often pests in fields and gardens. Tubers, such as those of the potato, are enlarged portions of underground branches in which a great amount of food is stored. The "eyes" of a potato contain buds each of which is capable of forming a shoot.

Many plants have very short stems that are partly or wholly buried in the ground. Short stems of this type are often associated with roots containing large reserves of food, as in the parsnip, carrot, beet, and dandelion. In other cases, such as the jack-in-the-pulpit and the crocus (Fig. 61), the short stem is itself the storage organ and is consequently enlarged and fleshy.

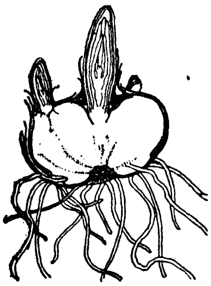


FIG. 61. The short, thick underground stem of a crocus, in vertical section.

According to their longevity, plants are classed as *annuals*, *biennials*, and *perennials.* Annuals live for but one season. They produce leaves, flowers, fruits, and seeds, and then die. In biennials, like the cabbage, turnip, and beet, the leaves formed the first year produce a quantity of food that is stored in the stem, leaves, or root, the storage organ or organs generally being thick and fleshy. The next year this stored food is used in the production of new organs, including flowers, fruits, and seeds, after which the plant dies. Perennials (plants that live for many years) may be either herbaceous or woody, woody perennials being trees, shrubs, or vines. Herbaceous perennials usually store reserve foods in underground stems, branches, or roots. Buds developed on these organs may grow into new shoots. The part of a herbaceous perennial which lives from year to year is usually, therefore, especially in temperate regions, an underground part, which may be a stem, part of a stem, a branch, or a root.

51. Functions of Stems. The chief functions of a stem or branch are the support of leaves and flowers, and conduction. Water with mineral nutrients in solution is conducted through the xylem and in the direction of the leaves. The foods made in the leaves pass through the conducting cells of the phloem to the parts of the plant where active growth is going on or where foods are being stored.

The green parts of a stem play a part also in the manufacture of foods, although in the sunflower, as in most familiar plants, it is chiefly in the leaves that this work is performed. In some plants, however, including cacti, practically all the foods are made

in the stem; in others, such as the asparagus, some of the branches do the work of food-making. Sometimes, as in the greenhouse "smilax," branches assume the form, as well as the functions, of leaves. In woody plants (trees and shrubs) it is often only the youngest branches that are green and therefore capable of manufacturing foods.

Usually some foods are stored for a longer or shorter time in certain parts of the stem, especially in the parenchyma of pith, cortex, and medullary rays. In many plants, especially those which live for more than a year, food-storage is an important function of the stem. For example, during the winter the parenchymatous cells in the stems of trees and shrubs often contain large amounts of starch and fats. The stem of the kohlrabi, potato tubers, and many other underground branches and stems are especially adapted for the storage of foods.

Summary

The growing apex of a stem includes an embryonic region, a region of elongation, a region of maturation, and a mature region. The three latter regions are differentiated into nodes and internodes. In the stems of dicotyledons and of gymnosperms the vascular bundles are arranged in the form of a hollow cylinder. In stems of monocotyledons the vascular bundles are as a general rule numerous and scattered.

Internodes of a dicotyledonous stem consist of stele, cortex, and epidermis. Tissues of the stele include pith, xylem, cambium, phloem, medullary rays, and pericycle. The cortex includes mechanical tissue, parenchyma, and endodermis. A node differs from an internode in that leaf traces are present in its cortex.

A stem of a dicotyledon or of a gymnosperm develops a cambium, the division of whose cells gives rise to secondary xylem and secondary phloem. The secondary xylem (with included medullary rays) formed in each growing season constitutes an annual ring. Annual rings are distinguishable because of differences in size between elements formed at the beginning and those formed at the end of the growing season. Older annual rings toward the center of a tree may be modified into heartwood. In such case, movement of sap is restricted to the outer annual rings, the sapwood.

Bark comprises all tissues outside the cambium. In a young stem the bark is composed of phloem, medullary rays, pericycle,

cortex, and epidermis. The bark of an older stem includes also a cork layer (or layers) produced by a cork cambium, which usually arises in the outermost portion of the cortex. Several successive cork cambiums may be formed by a stem. Lenticels may be present in the outer surface of the bark.

Internodes of monocotyledons are ordinarily not sharply differentiated into cortex and stele. In the numerous scattered vascular bundles there is no cambium between xylem and phloem. Most monocotyledonous stems have no secondary thickening. Those which thicken secondarily have a cambium which produces new vascular bundles. A wounded portion of a stem may form a wound tissue (callus).

Branch primordia are formed in the embryonic region in the axils of leaves. A branch primordium may develop immediately into a branch or may remain dormant for one or more years.

According to proportion of wood and length of stem, plants are classed as trees, shrubs, and herbs. A plant whose stem can not hold itself erect may creep or clamber; if the stem can attach itself to a support and so grow upward, the plant is a vine. Vines may be woody or herbaceous. Stems that grow underground are either erect or horizontal. They may be entirely subterranean, or may produce aërial branches. According to their longevity, plants are classed as annuals, biennials, and perennials.

The functions of a stem include support of leaves and flowers, conduction of materials, manufacture of foods, and storage of foods.

CHAPTER VI

BUDS

52. Nature and Positions of Buds. As noted in § 34, the embryonic region of a stem or branch gives rise to numerous leaf primordia (Fig. 62). Immediately below the apex of the embryonic region such primordia are but small humps of embryonic tissue. Farther back from the apex the young leaves, developed from these primordia, have grown more rapidly in length than the embryonic region of the stem, and, since their growth has been more rapid on their outer than on their inner surfaces, they have curved so as to enclose the embryonic region. Such a terminal portion of a stem or of a branch with its unelongated internodes bearing immature leaves, or immature and mature leaves, which curve and enclose the growing point, is termed a *bud.*

New growing points which develop into buds arise also in the axils of many leaves, usually a single growing point in an axil. Buds that develop from such growing points are called *axillary buds* to distinguish them from the *terminal bud* of a stem or branch. An axillary bud is often inconspicuous until the leaf in whose axil it occurs has fallen (Fig. 63).

53. Naked Buds. If the leaves borne by a bud are all foliage leaves, the bud is *naked.* Naked buds are characteristic of all annuals, of most biennials, and of a few perennials such as Elodea (Fig. 62), juniper, and the staghorn sumac. During the growing period, new leaf primordia, nodes, and internodes are being formed in the anterior portion of a bud. Farther back in the bud the internodes undergo elongation and the leaf primordia grow into young leaves. As a result of the continuation of these activities during the growing period, such a naked bud is constantly changing in its composition of leaves, nodes, and internodes. In the axils of leaves within the bud may be the primordia of branches. In some few plants the older internodes elongate but slightly as new leaf primordia and internodes develop in the embryonic region. The result is a continual increase in the size of the bud which may, as in the head lettuce, become relatively enormous.

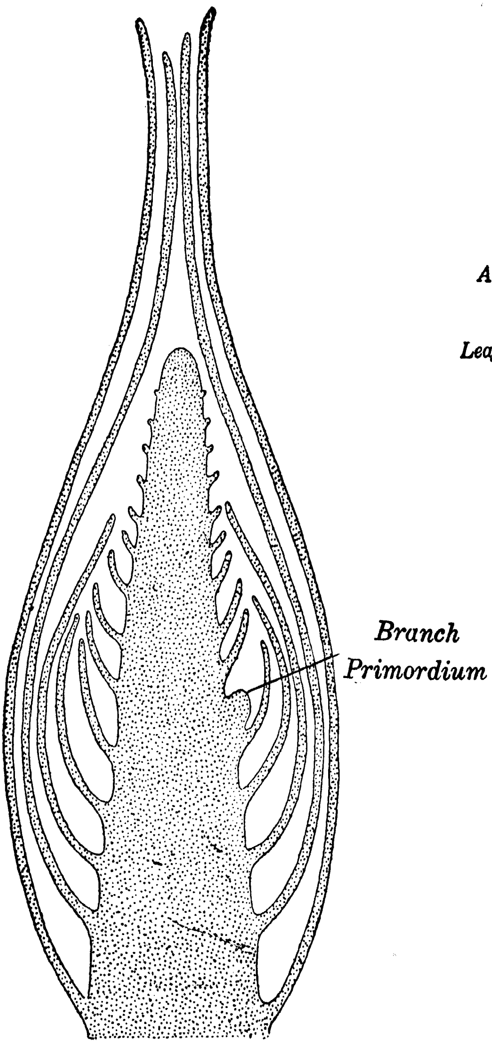


FIG. 62. Lengthwise section through a terminal naked bud of Elodea (diagrammatic).

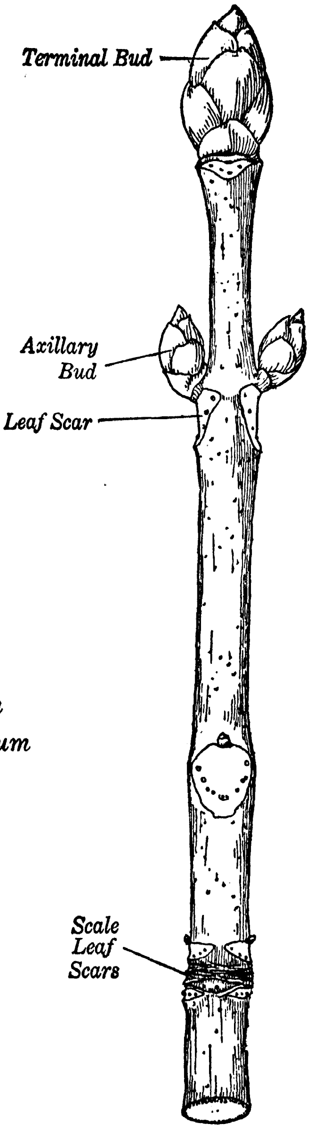


FIG. 63. A branch of the horse-chestnut bearing terminal and axillary protected buds.

Naked buds are of various types as regards the immature parts which they contain. Some are *leaf buds;* such a bud (Fig. 62) includes an embryonic branch or stem tip with its nodes and unelongated internodes and the primordia of leaves. At some of the nodes may appear the primordia of branches. Other naked buds are

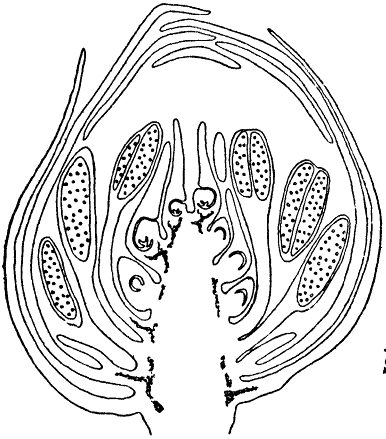


FIG. 64. Lengthwise section of an axillary naked floral bud of the buttercup, containing the parts of a single flower enclosed by foliage leaves (diagrammatic).

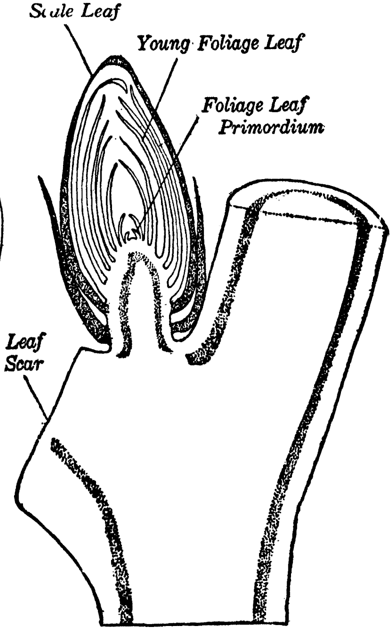


FIG. 65. Lengthwise section through an axillary protected leaf bud of the elm (diagrammatic).

floral buds. A floral bud contains the primordia of a flower or of a cluster of flowers borne on an embryonic branch. A floral bud of a buttercup (Fig. 64) contains the embryonic parts of a single flower; one of a sweet pea possesses the embryonic parts of a cluster of flowers. If, as happens in some instances, a floral bud contains primordia of leaves and possibly of branches in addition to those of a flower or flowers, it may be called a *mixed bud.* These three types of buds to some extent intergrade; hence the names applied to them should be regarded not as exact but rather as convenient and general expressions of differences.

In contrast with the *active* naked buds just described are those which enter upon a period of rest or of very slow development. It is in such a resting condition that the naked buds of most bi-

ennials, as for example the cabbage, pass the winter. Certain perennials also, including Elodea, have resting naked buds at the tips of stems and branches during the winter.

54. Protected Buds. If the outermost leaves of a bud, instead of being foliage leaves, are scale-like, it is a *protected bud.* Most woody perennials of temperate regions, such as the elm, hickory, and horse-chestnut (Fig. 63), form buds of this type. In such a bud the outermost scale leaves commonly overlap and are often heavily cutinized or covered with waxy or resinous substances. In addition, numerous hairs may be borne on the surfaces or margins of the scales. Such secretions and outgrowths tend to prevent the loss of water and the consequent drying out of the enclosed immature parts of the bud. They also afford protection against mechanical injury.

FIG. 66. Lengthwise section of an axillary protected mixed bud of the apple (diagrammatic).

As regards the immature parts that they contain, protected buds like naked buds may be either leaf buds, floral buds, or mixed buds. For example, the elm has both leaf buds (Fig. 65) and floral buds, a floral bud containing the embryonic parts of a cluster of flowers (see also Fig. 68). The apple (Fig. 66), lilac, and horse-chestnut form mixed buds.

55. Unfolding of Protected Buds (Fig. 67). Protected buds, at least in temperate regions, ordinarily undergo a period of rest during the winter and resume growth with the coming of spring. When a protected leaf bud resumes growth the scale leaves expand. Sooner or later the scale leaves are shed. The opening of a bud is accompanied by a very rapid elongation of the internodes within it and by a rapid development of the embryonic foliage leaves to maturity. This rapid maturation of embryonic leaves accounts for

the suddenness with which a tree puts forth a crop of new leaves in the spring. All the leaves borne by some trees, such as the horse-chestnut, were present in an immature condition in protected buds at the beginning of the growing season; in other trees, such as the elm, additional foliage leaves are formed from the embryonic regions of stem and branches after the maturation of such immature leaves as were present in the dormant protected buds.

After the shedding of the scale leaves a scar remains on the stem or branch marking the former place of attachment of each scale.

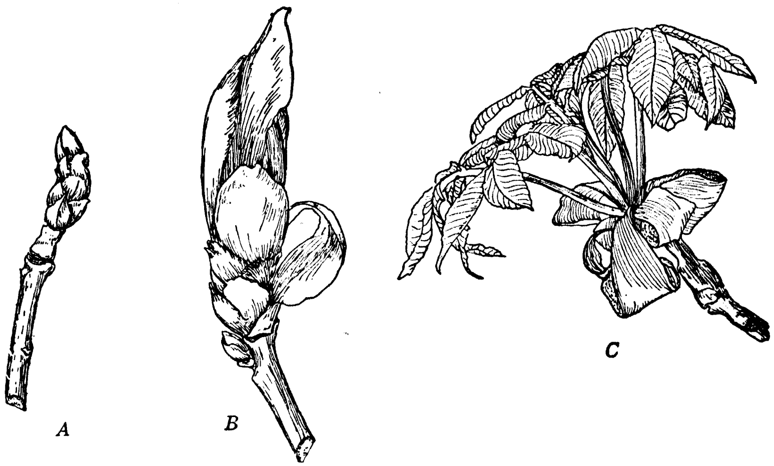


FIG. 67. Protected leaf buds of the hickory in different stages of development. *A*, winter condition. *B*, beginning of elongation in the spring; scale leaves greatly expanded. *C*, after the foliage leaves have emerged; scale leaves still present.

Since the internodes between the scale leaves elongate but slightly, the scars left by the scales form a ring about the stem (Fig. 63). In geographical regions where scale leaves are shed but once a year, it is therefore possible to gauge the age of a branch by counting the groups of scale-leaf scars.

Protected leaf buds may be either terminal or axillary. Those which elongate are usually at or near the apex of the stem or branch; the remaining leaf buds—*latent buds*—ordinarily do not open and elongate. Under changed circumstances latent buds may develop into branches, as, for example, when the active buds above them are destroyed. Buds may thus be stimulated to development after years of latency.

Protected floral buds are usually axillary. When such a bud opens, the scale leaves, as in the case of leaf buds, expand and fall

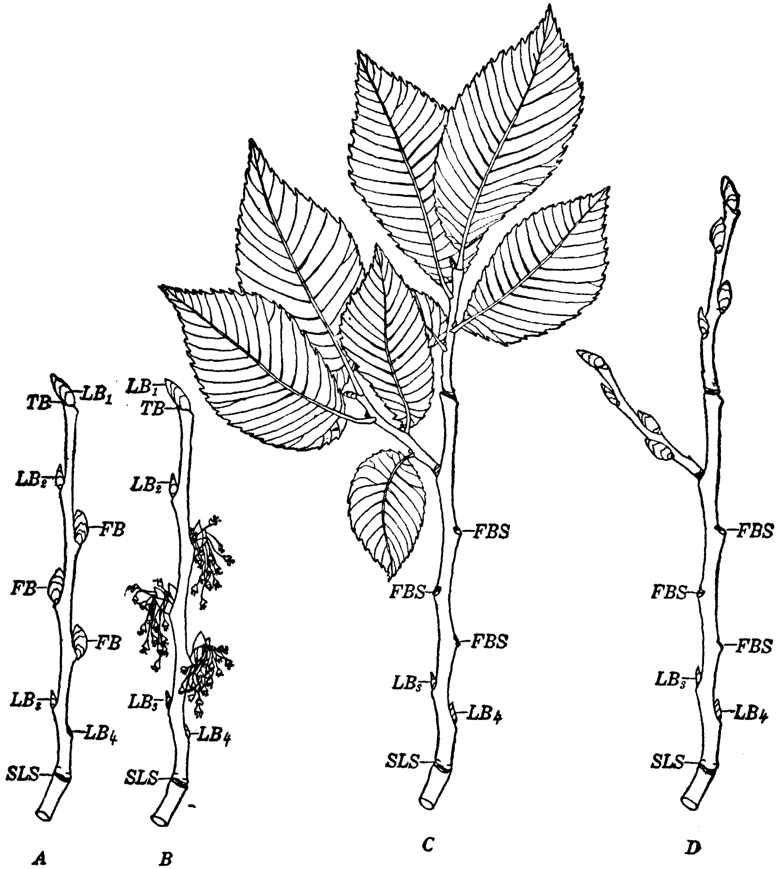


FIG. 68. The seasonal history of an elm twig and of its protected buds. *A*, winter condition. *B*, early spring; the floral buds have developed into floral branches. *C*, midsummer; 2 axillary leaf buds have developed into branches and produced leaves; 2 have remained latent; the floral branches have developed mature fruits and have fallen, leaving scars. *D*, late autumn; the leaves have fallen; in their axils are protected leaf and floral buds. *TB*, minute undeveloped terminal bud; LB_1–LB_4, axillary leaf buds; *FB*, axillary floral buds; *SLS*, scale-leaf scars; *FBS*, floral branch scars.

off, leaving a group of scale-leaf scars. The embryonic branch within the bud elongates somewhat and the floral primordia which it bears develop into one or more flowers. The unfolding of floral

buds frequently occurs before the unfolding of the leaf buds. Indeed, as in the elm (Fig. 68), the flowers may produce mature fruits and the fruits may be shed by the time the foliage leaves have come to maturity. In other cases, as in the cherry, the fruits do not mature until some weeks after the foliage leaves have matured.

In the unfolding of a protected mixed bud, floral and leaf primordia may mature simultaneously, or the floral primordia may mature more rapidly than those of the leaves. The horse-chestnut is an example of the former type; the apple, of the latter.

56. Adventitious Buds. It is possible for new growing points to become organized in various parts of a plant other than the axils of leaves. Buds that develop from these new growing points are similar in structure to the terminal and axillary buds already described and differ only in the position in which they are borne on the plant. Such *adventitious buds* may arise from various tissues of a leaf (as in begonia); from the cortex of a stem; from the pericycle of a stem or root; or from wound tissue of a stem or root. The sprouts which appear on the cut surfaces of stumps of trees of many kinds result from the elongation of adventitious buds.

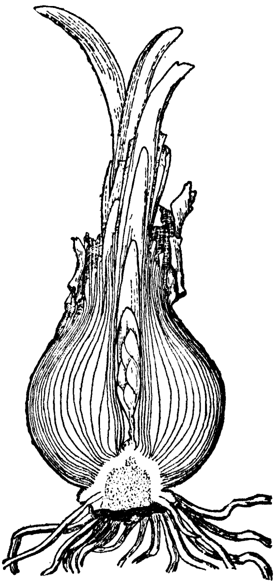


FIG. 69. The bulb of a hyacinth in lengthwise section.

57. Bulbs. Some plants produce a special type of underground bud commonly known as a *bulb.* Among such plants are the hyacinth, narcissus, onion, and tulip. A median lengthwise section (Fig. 69) of one of these bulbs shows that it has a short conical stem. The upper surface of the stem bears numerous broad, fleshy scale leaves enclosing the terminal growing point and, in some plants at least, the primordia of foliage leaves and flowers. Many of the scale leaves are storage organs containing abundant reserve food, often in the form of sugar. From the outer lower edge of the stem grow many adventitious roots. Among the new growing points which arise in the axils of the scale leaves, an

occasional one may itself develop conspicuous scale leaves and so become a new bulb.

Unlike those of other protected buds, the scale leaves of a bulb never unfold when growth is resumed. At this time the foliage-leaf primordia, if present, as in the narcissus, develop rapidly into foliage leaves. From the central region of the growing point arises a floral axis which bears a single flower as in the tulip, or a cluster of flowers as in the hyacinth.

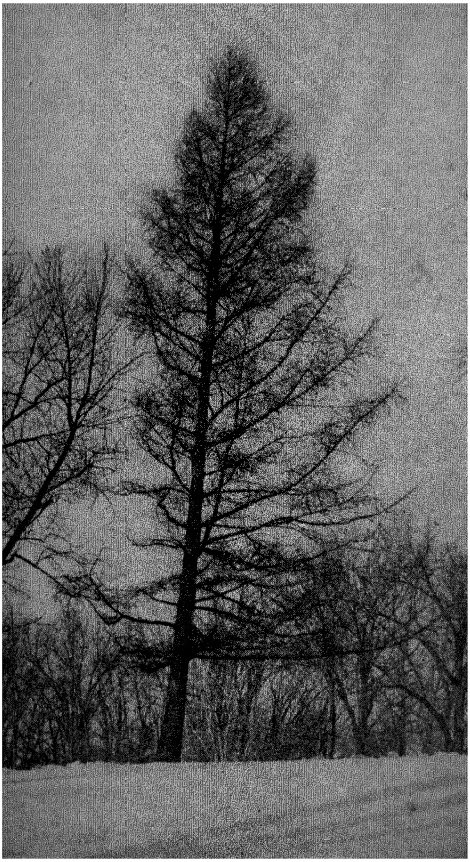


FIG. 70. The larch, a tree with a conspicuous central shaft; growth from the terminal bud of the stem is more rapid than from the terminal buds of branches.

58. Buds and Plant Form. The form characteristic of a plant is an expression of the type and degree of the development which has taken place from its buds. Many conifers, such as the pine, spruce, and larch (Fig. 70), produce strong terminal protected buds and, in close proximity to each terminal bud, several smaller axillary protected buds. During successive growing seasons development from the terminal bud of the stem is more rapid than that from the terminal buds of the branches, with the result that a single strong central shaft or trunk is produced. Trees like the maple (Fig. 71) and the elm (Fig. 72), although

they have a different arrangement of buds, show much the same growth tendencies but to a lesser degree; consequently, growth of one or more of the lateral branches may be nearly or quite as rapid as that of the original trunk, and thus several large branches are formed. The tendency for many axillary buds on these branches to elongate results finally in the production of a much-branched, spreading top, very different from that of a spruce or larch.

FIG. 71. The maple, a tree in which the terminal growth of branches is nearly as active as that of the central axis. Photograph by George Kemmerer.

Sometimes, as in the lilac, a mixed bud often occupies the terminal position on each of the larger branches. Since this bud terminates in a cluster of floral primordia, further extension of the vegetative parts of the plant must be brought about by growth from axillary buds. If many of these axillary buds elongate, a densely branching plant is produced. Some plants, like the elm (Fig. 68) and the poplar, have many axillary floral buds and relatively few axillary leaf buds back of each terminal bud. Later in the same spring the floral branches, now bearing fruits, fall from the tree, leaving conspicuous bare spaces on the twigs which bore them.

Although each kind of tree tends to develop a characteristic form, it must not be overlooked that environmental factors also play an important rôle in determining the shape of the tree. Among these environmental factors are wind, shade, and temperature (see Fig. 55). The form of a tree may be profoundly influenced by the presence of surrounding vegetation. A pine tree growing in the open takes a very different form from that which it would assume in a dense forest. The effects of the human element in the environment are illustrated by the re-

sults of pruning, sometimes resulting in the production of bizarre forms.

Summary

Buds may be either terminal or axillary. Either terminal or axillary buds may be naked or protected. Whether terminal

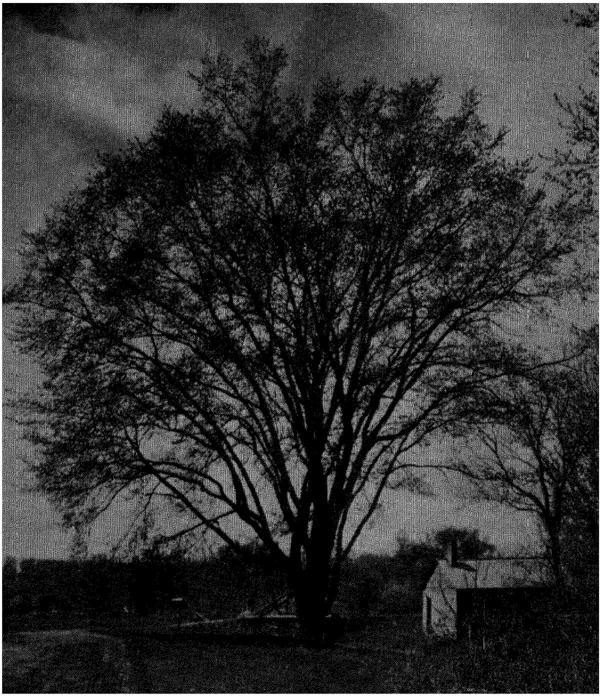


Fig. 72. The elm, whose habit of growth is similar to that of the maple. Photograph by George Kemmerer.

or axillary, naked or protected, a bud may be a leaf bud, a floral bud, or a mixed bud.

Naked buds, while for the most part actively growing, may in some plants remain for a time dormant. Protected buds in general, at least in temperate regions, undergo a dormant period. Some protected buds remain indefinitely in a latent condition unless induced to develop by some special stimulus.

When a protected bud opens, the scale leaves fall, leaving

scars at their former places of attachment. The primordia (of leaves, branches, or flowers) previously enclosed within the scales then develop.

Buds which appear in other places than at the ends of stems or branches or in the axils of leaves are adventitious.

A bulb is a special type of underground bud.

The form of a plant is determined by the type and degree of the development that takes place from its buds.

CHAPTER VII

LEAVES

59. Development of Leaves. Leaves are first recognizable as small dome-shaped primordia along the sides of the embryonic region of a stem or branch. In most cases the continued division of cells in a leaf primordium results in the development of a young leaf which, though composed of embryonic cells, has much the form that will characterize it at maturity. Approximately the number of cells that will be present in the mature leaf is reached while the cells are still embryonic and the leaf is small. The rapid increase in size of an unfolding leaf is due, therefore, not chiefly to the formation of new cells, but to the enlargement and maturation of embryonic cells already formed; in consequence, all the cells enlarge and mature simultaneously, and there are no localized regions of elongation and maturation. The lack of such distinct regions is one important respect in which the development of most leaves differs from that of a root, stem, or branch. Another important difference lies in the fact that in general the cells of a leaf are formed once for all, cell division then ceasing; whereas division, and therefore growth, may continue indefinitely in the apical region of a root or stem.

In certain monocotyledons, however, especially in some grasses, the basal portion of each leaf remains embryonic even after the apical portion is mature. The leaf continues to grow in length as cells formed in the basal embryonic region successively enlarge and mature.

60. Arrangement. The arrangement of leaf primordia on a stem or branch (as well as of the leaves developed from these primordia) varies greatly as between different species, and may vary considerably on different parts of a single plant. In some plants, leaves are borne in pairs at each node and *opposite* each other (Fig. 73, *D*), each pair usually standing at right angles to the pair below. Coleus, maples, and lilacs have leaves arranged in this way. If three or more leaves are borne at a single node, as in Elodea, they are *whorled*.

Leaves are *alternate* when but a single leaf occurs at each node and the leaves follow each other on the stem in a spiral manner; that is, a line drawn from any leaf-insertion to the next above, and so on, forms a spiral around the stem. An arrangement of

FIG. 73. Types of leaf-arrangement. *A*, *B*, *C*, various alternate arrangements. *D*, opposite arrangement. The upper figure in each case represents the leaf-arrangement as seen from above.

this nature is most common. In a species whose leaves are alternately arranged, the distance around the stem from any one leaf-insertion to the next is substantially equal, although the vertical distance from leaf to leaf may vary greatly. In some plants, as the grasses and elms, the second leaf is on the side opposite the first and the third on the side opposite the second—that is, directly over the first (Fig. 73, *A*). In other plants, as the hazel, each leaf is one third the distance around the stem from the leaf next below (Fig. 73, *B*). In still other plants, as the cherry, apple, and willow, any two successive leaves are separated by two fifths of the circumference of the stem (Fig. 73, *C*). In the latter case a spiral con-

necting the leaves passes twice around the stem before a leaf is reached which is directly over that with which the spiral started. In still other plants, more than two turns of a spiral are necessary to reach a leaf directly above that with which the spiral began.

In many common plants each leaf is so located as to shade its neighbors as little as possible. If leaves are numerous, nearly

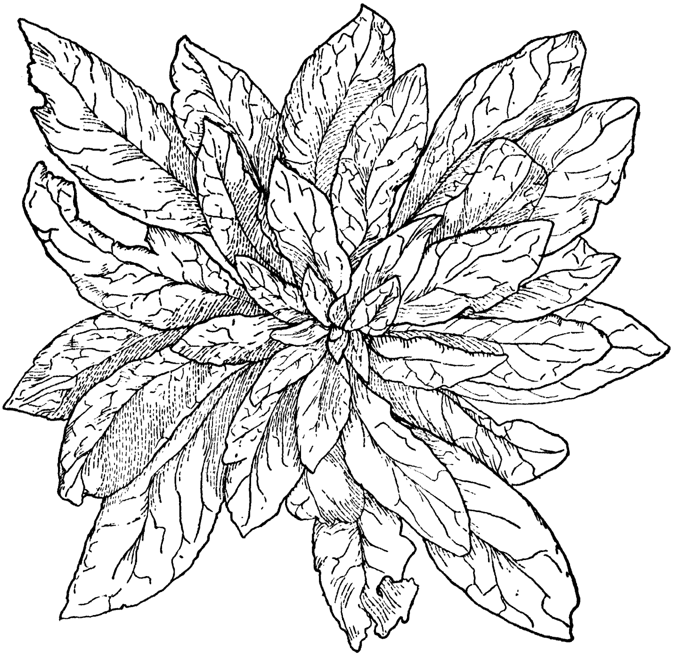


FIG. 74. The rosette arrangement (leaf mosaic) of the first-formed leaves of a mullein.

all the space exposed to light is occupied. A leaf-arrangement of this nature is spoken of as a *leaf mosaic.* When Japanese ivy grows upon a wall, it furnishes a striking example of a mosaic. Leaves that lie prostrate on the ground, such as those of the dandelion or the basal leaves of the mullein (Fig. 74), form a rosette whose lower leaves are longer than those above, the greater length of the lower leaves being chiefly in their petioles.

61. External Structure. Most leaves are made up of certain definite parts which are externally recognizable. Often a foliage leaf is composed of *blade, petiole,* and *stipules;* many foliage leaves,

however, lack petioles, stipules, or both. In the grasses and in some other monocotyledons, both petiole and stipules are lacking and, as illustrated by the corn, the basal part of each leaf is a sheath.

The petiole may be short or long, stout or slender, cylindrical or flattened, and in some cases grooved or winged. At its base, where it is attached to the stem, the petiole may be swollen or may clasp or ensheathe the stem. When a petiole is lacking and the blad is attached directly to the stem, the leaf is *sessile*. The blades of some sessile leaves partly surround the stem, as in the wild lettuce; or, as in the bellwort (Fig. 75, *A*), they completely encircle the stem. When sessile leaves are opposite, the blades of a pair may be united around the stem, as in some of the wild honeysuckles (Fig. 75, *B*).

FIG. 75. *A*, stem of the bellwort with leaves which encircle the stem. *B*, stem of a climbing honeysuckle with opposite leaves, the two of each pair united about the stem.

Stipules may be either blade-like or spine-like. When present they are borne one on either side of the base of the petiole. Certain blade-like stipules are green and, like the leaf blade, manufacture foods. In this respect such stipules are usually of minor importance as compared with the blade, but in the pea (Fig. 76, *A*) and in some other plants their importance in food-manufacture approaches that of the rest of the leaf. Other blade-like stipules furnish a protective covering for immature leaves and, as in certain oaks and willows, are shed after the leaves are mature. The common black locust and certain Euphorbias (Fig. 76, *C*) are examples of plants whose stipules are spine-like and persist after the other parts of the leaves are shed.

In spite of great variation between plants of different kinds in shape of leaf blades, the arrangement of the veins is according to one of two main plans. In the majority of monocotyledons, as in the corn and the lily of the valley (Fig. 77, *A*), several main

veins run approximately parallel to the leaf axis, extending from the base to the apex of the blade. Such leaves are *parallel-veined.* The leaves of the banana (Fig. 77, *B*) and of some other mono-

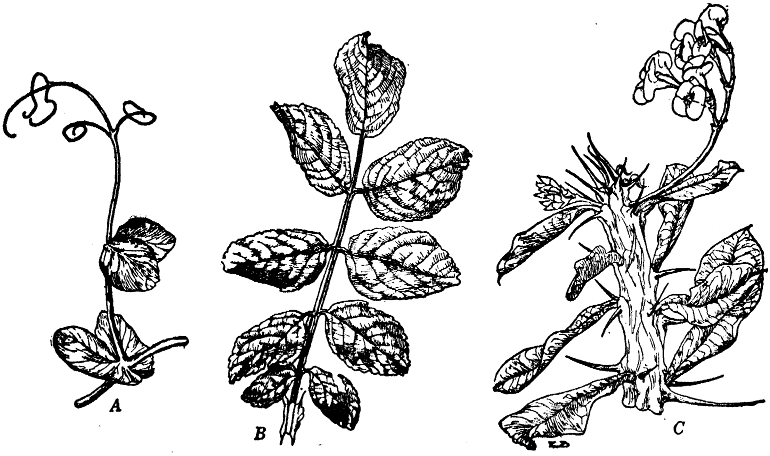


FIG. 76. Leaves with stipules. *A*, leaf of the pea; some leaflets replaced by tendrils. *B*, rose leaf. *C*, twig of a Euphorbia, with spine-like stipules.

cotyledons show a deviation from the ordinary parallel-veined arrangement. The leaf blade of such a plant has a midrib and many branch veins; the latter extend, parallel with one another, from the midrib nearly or quite to the margin. In both types of parallel-veined leaves the conspicuous veins really give off many fine branches which constitute a network; but these slender branches are not readily visible.

In the second main plan of vein-arrangement, which is characteristic of the leaf blades of the majority of dicotyledons, the main vein (midrib) or main veins branch repeatedly, many of the ultimate branches meeting one another so as to form a rather conspicuous network

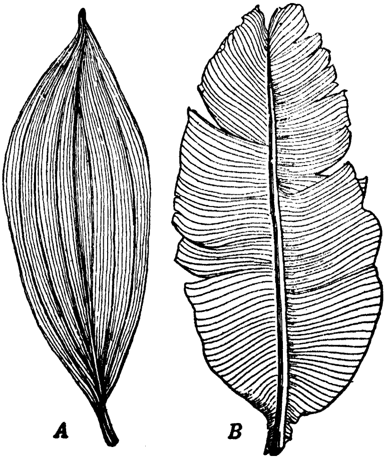


FIG. 77. *A*, parallel-veined leaf of lily of the valley. *B*, pinnately parallel-veined leaf of banana.

(Fig. 78). Such leaves are *netted-veined.* A netted-veined leaf with a conspicuous midrib, from different points on which large branch veins diverge, as in a leaf of the elm (Fig. 79, *A*), is *pinnately* netted-veined. If several main veins diverge from a single point at the base of the leaf, as in the maple (Fig. 79, *B*), the arrangement of veins is *palmate.*

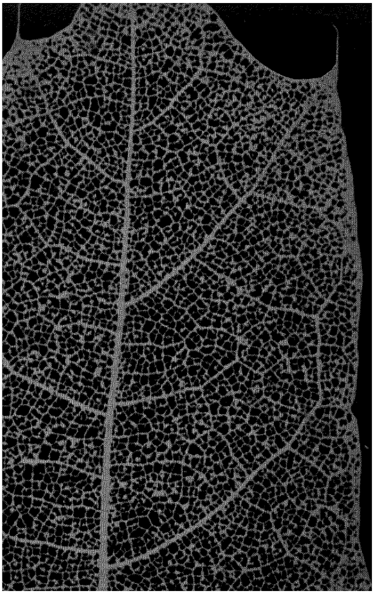


FIG. 78. The system of veins of a netted-veined leaf (black oak).

In leaves the margins of whose blades are lobed, the method of lobing usually corresponds to the arrangement of the veins; hence, if a leaf is pinnately veined, it may be pinnately lobed. If the veins are palmately arranged, the leaf may be palmately lobed. In case the lobing extends to the midrib or to the base of the blade, the leaf is *compound;* the parts into which the blade is thus divided are *leaflets.* If the various leaflets are sessile upon the midrib or upon the petiole, it may be difficult to distinguish between a compound and a deeply lobed leaf. No such difficulty obtains, however, in compound leaves each of whose leaflets has a separate stalk. Compound leaves may be *pinnately* compound, like those of the ash (Fig. 80, *A*), the rose (Fig. 76, *B*), and the pea (Fig. 76, *A*); or *palmately* compound, like those of the horse-chestnut (Fig. 80, *B*). The leaflets may themselves be divided, as in many ferns. Some compound leaves are three times divided, and the common meadow rue (Fig. 80, *C*) has a four-times-divided leaf.

The surface of the blade of a foliage leaf may be smooth, rough, or hairy. The surfaces of most leaves are cutinized, and some are coated with wax; when the waxy coating is broken up into minute rods or plates it appears as a "bloom," like that on the leaves of the cabbage and the tulip. The blades of many young leaves are densely covered with hairs which check, more or less, the evapo-

ration of water from the immature blades. As a blade matures, the hairs may shrivel and disappear, or they may persist. Some leaf

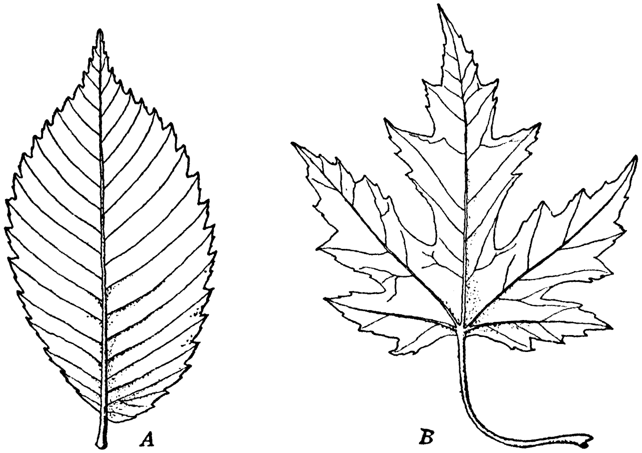


FIG. 79. *A*, elm leaf, with pinnate venation. *B*, leaf of maple, palmately lobed and with palmate venation. Only the larger veins are shown in each case.

blades, like those of the mullein, are covered by a dense matting of hairs (Fig. 81, *G*). The leaves of some plants bear glandular

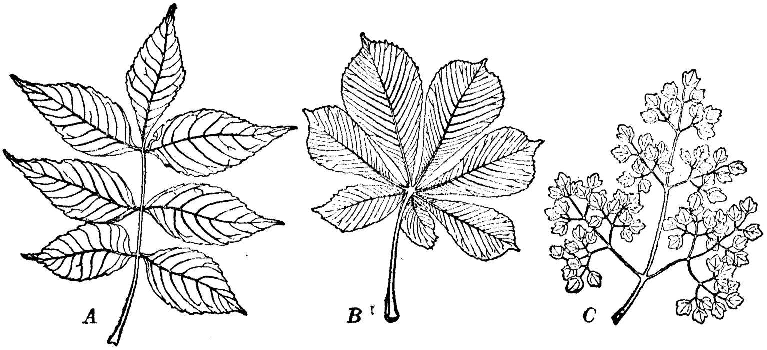


FIG. 80. Compound leaves. *A*, pinnately compound leaf of an ash. *B*, palmately compound leaf of the horse-chestnut. *C*, four-times-divided leaf of meadow rue.

hairs (Fig. 81, *E*, *F*) which secrete special substances. The strong odors given off by mints are due to volatile oils secreted by the terminal cells of glandular hairs on the leaves and stem.

62. Tissues of a Leaf Blade. The blade of a dicotyledonous leaf (Fig. 82) typically includes several distinct tissues. On its upper side is an *epidermis,* whose cells are often irregular as seen in surface view but appear nearly rectangular in cross section. The outer walls of these epidermal cells are cutinized. Next beneath the upper epidermis is a layer (or under certain conditions two or more layers) of *palisade cells,* the long axis of each cell being perpendicular to the surface of the leaf; these cells are frequently separate from one another at their lower ends. The palisade cells contain many small chloroplasts. Next beneath them, commonly making

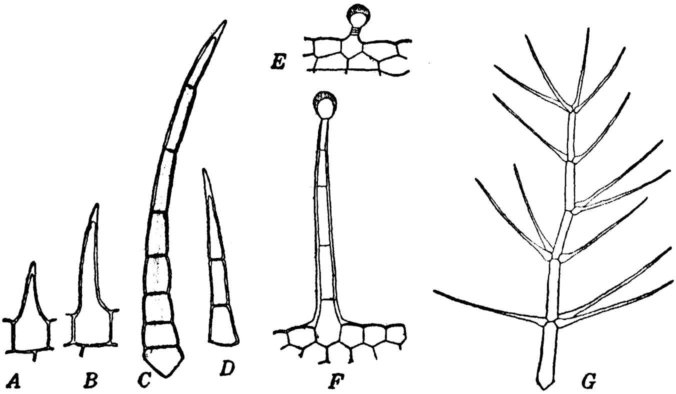


Fig. 81. Epidermal hairs from various leaves. *A–D,* from the sunflower. *E, F,* young and old glandular hairs of the geranium. *G,* branching hair of the mullein.

up the greater part of the thickness of the leaf, are several layers of rounded or irregularly shaped cells, constituting the *spongy tissue;* between these cells are numerous, often large, *intercellular spaces.* The cells of the spongy tissue also contain chloroplasts, though usually not so many in proportion to their size as do the palisade cells. Adjoining the spongy tissue is the *lower epidermis,* whose cells are similar to those of the upper epidermis. Here and there in the lower epidermis is an opening called a *stoma* (plural, *stomata*). Each stoma lies between two almost crescent-shaped *guard cells* which are smaller than the other cells of the epidermis and which contain chloroplasts. The stoma opens into an intercellular space, which in turn is continuous with spaces between the cells of the spongy tissue. All the intercellular spaces in the spongy tissue are likewise connected with one another and with

such spaces as occur between the palisade cells. Thus the stomata and the intercellular spaces constitute an aërating system, by means of which gases may be freely interchanged between the atmosphere and the interior cells of the leaf. In many leaves stomata are present also in the upper epidermis.

Both upper and lower epidermis may bear hairs. Some hairs are merely single elongated epidermal cells. In other cases a hair

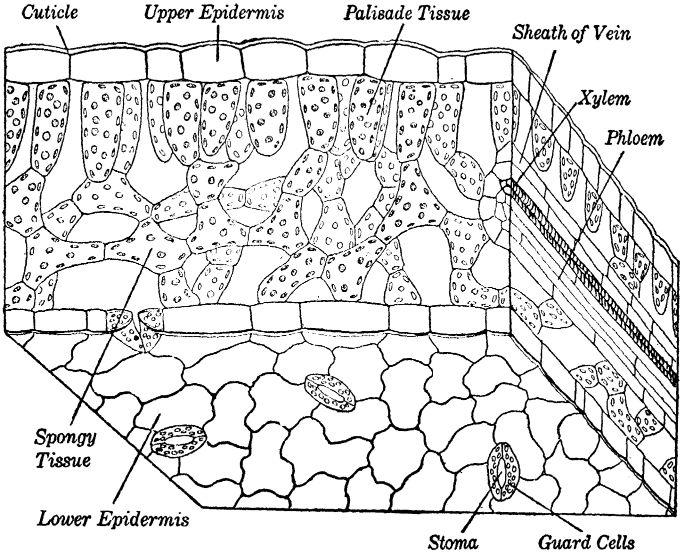


FIG. 82. Portion of the blade of a sunflower leaf, showing the relations of the various tissues.

is a row of two or more cells resulting from the growth and division of an epidermal cell. In still other instances a hair is composed of more than one row of cells.

The veins of a leaf are vascular bundles which are continuous through the petiole with the vascular bundles of the stem. Like a stem bundle, a vein contains xylem and phloem, the xylem being toward the upper side of the blade and the phloem toward the lower surface. Xylem and phloem consist, respectively, of the same types of elements as are found in the bundles of the stem. As the branches from the midrib and the main veins become progressively smaller, the phloem and xylem contain fewer and smaller elements. Each of the ultimate veinlets in which the system terminates may possess no phloem and but a single tracheid. Surround-

ing the xylem and phloem of a vein is a sheath whose thickness varies with the size of the vein. In the case of the midrib, and often of some of the larger veins, the sheath is usually a compact mass of cells extending from upper to lower epidermis, consisting of parenchyma and mechanical tissue, and occupying in this particular region the place of palisade and spongy tissue. The sheath about one of the smaller veins or veinlets consists usually of but a single layer of parenchymatous cells and lies wholly within the spongy tissue.

63. Tissues of a Petiole. The vascular bundles of a petiole run lengthwise from the junction of the petiole with the stem to its junction with the leaf blade. A petiole may contain one, three, five, or more bundles. If more than one is present, the various bundles may be parallel throughout the length of the petiole, or they may lie so close to one another that at the outer end of the petiole they appear to be a single bundle. As seen in cross section (Fig. 83), the separate bundles in the petiole usually lie in an arc which is concave toward the upper side of the petiole.

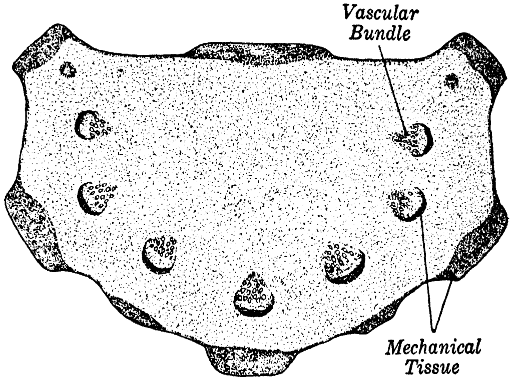


FIG. 83. Diagram of a cross section through the petiole of a leaf of the beet.

Petiolar bundles, like leaf veins, contain xylem and phloem. The phloem provides a pathway for the transfer to the stem of food manufactured in the blade; the xylem provides a pathway for the transfer of water and mineral nutrients from stem to blade. Surrounding each bundle is often a sheath of thick-walled mechanical cells. There may be mechanical tissue also just within the epidermis of the petiole. Both systems of mechanical tissue aid materially in the functioning of the petiole as a support for the blade. The remaining cells of the petiole, except the epidermis, are parenchymatous.

64. Variation in Foliage Leaves. It has been suggested in previous paragraphs that leaves borne by plants of different kinds

often differ greatly in form, structure, and even in function. Such variations are due chiefly to differences in the arrangement and

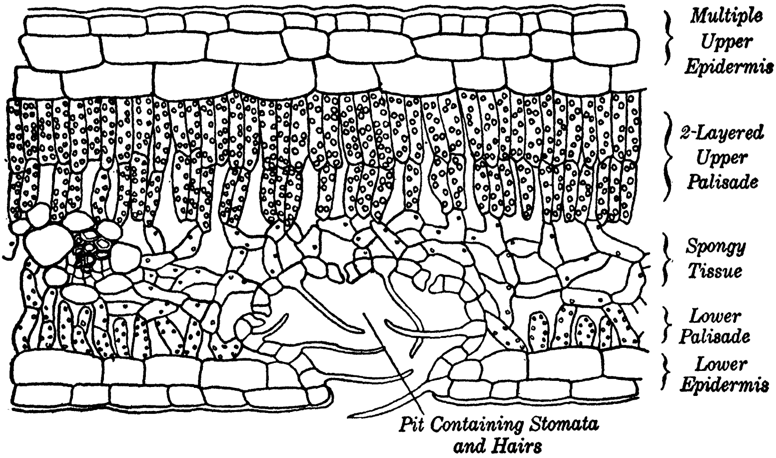


FIG. 84. Cross section of a portion of an oleander leaf.

proportions of the various tissues rather than to the presence of tissues of different sorts. A special type of arrangement is found in such leaf blades as those of the oleander (Fig. 84) and the rubber

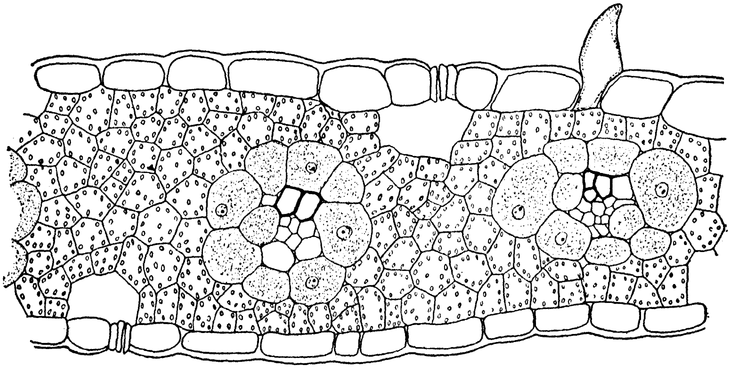


FIG. 85. Portion of a cross section of a corn leaf.

plant, which have a palisade layer next the lower, as well as one next the upper epidermis, the spongy tissue thus lying between two palisade layers.

Some leaf blades lack certain of the tissues that have been de-

scribed. Many plants, like the compass plant and Eucalyptus, whose leaf blades are vertical rather than horizontal, have no spongy tissue, all the chloroplast-containing cells within each blade being palisade-like and perpendicular to the epidermis. In other leaves, like those of the grasses, the interior chloroplast-bearing region is not clearly differentiated into palisade and spongy

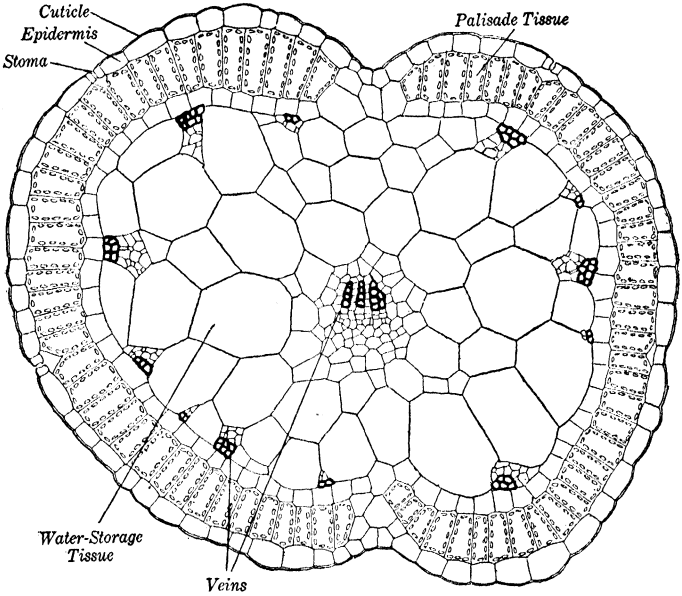


FIG. 86. Cross section of a leaf of the Russian thistle, with large parenchymatous water-storage cells.

tissues. In the corn leaf (Fig. 85), for example, intercellular spaces occur only immediately within the stomata, which are very numerous on both sides of the leaf; the remaining tissue between upper and lower epidermis, apart from the veins, is composed of compactly arranged cells with numerous chloroplasts.

Ordinarily the foods manufactured in a foliage leaf do not remain long in the leaf but are transferred to, and stored in, some other organ such as root or stem. Sometimes, however, as in the cabbage and the century plant, considerable amounts of foods are stored in foliage leaves, which in such plants are usually relatively thick.

The foliage leaves of many plants characteristic of dry regions

have thick, fleshy leaves composed in the main of a water-storage tissue. This tissue may be an epidermis several cells in thickness, as in the leaf of the begonia; but more commonly the water-storage tissue is internal, as in leaves of the Russian thistle (Fig. 86), the century plant, and the aloe (Fig. 87). In either case the storage tissue is composed of large parenchymatous cells with few or no chloroplasts. The imbibing power of mucilaginous substances in the dense cytoplasm and in the central vacuoles of these cells greatly increases their water-absorbing and water-retaining capacity. Water so held within the storage tissue may, however, move to other parts of the plant after the water supply of the soil is exhausted, thus keeping the plant alive for some time.

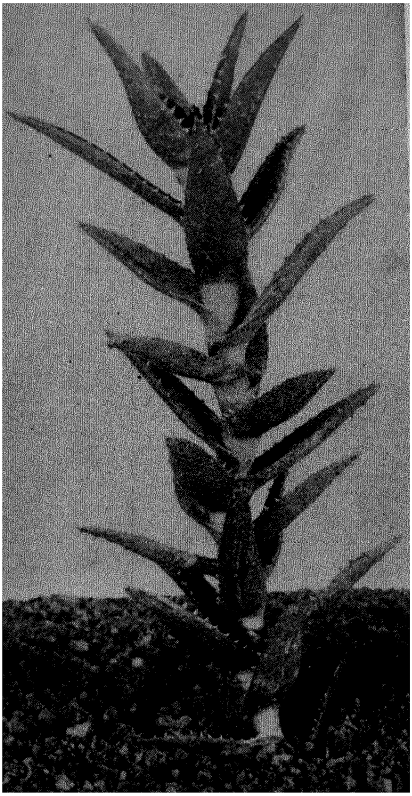


FIG. 87. An aloe, in whose thick leaves considerable amounts of water are stored.

The leaves of certain plants obtain a part of their food from the bodies of insects. An example is the common pitcher plant (Fig. 88) growing in marshes, whose pitcher-like leaves are usually partly filled with water. On the inside of the tip of each leaf are stiff hairs pointing inward and downward, and glands which secrete a fluid attractive to insects. After insects enter the pitcher, some of them are prevented by the hairs from escaping, and many insects ultimately drown in the water at the base of the pitcher. Substances from their decomposing bodies are used as foods by the plant. Another plant growing in similar situations is the sun-

dew (Fig. 89). Its leaves are provided with slender, sticky hairs which are sensitive to contact with protein-containing bodies. If a small insect touches one of the hairs it sticks to the hair, and in its struggles comes into contact with neighboring hairs which then bend over and hold the insect fast. After the death of the insect,

FIG. 88. A pitcher plant (Sarracenia).

the soft parts of its body are dissolved by secreted digestive juices. In time the hairs resume their ordinary position.

65. Variation in Leaves on the Same Plant. Foliage leaves borne on different parts even of the same plant may differ considerably in form and structure. The leaves of a tree that are freely exposed to sunlight frequently have a thick, heavily cutinized epidermis, a two- or three-layered palisade tissue, and a spongy tissue with small intercellular spaces; whereas leaves in the interior of the crown of the same tree may have a thinner, less heavily cutinized epidermis, a single palisade layer, and a spongy tissue with large intercellular spaces.

Even more striking differences appear between the aërial and the submerged leaves of some water plants. The aërial leaves of

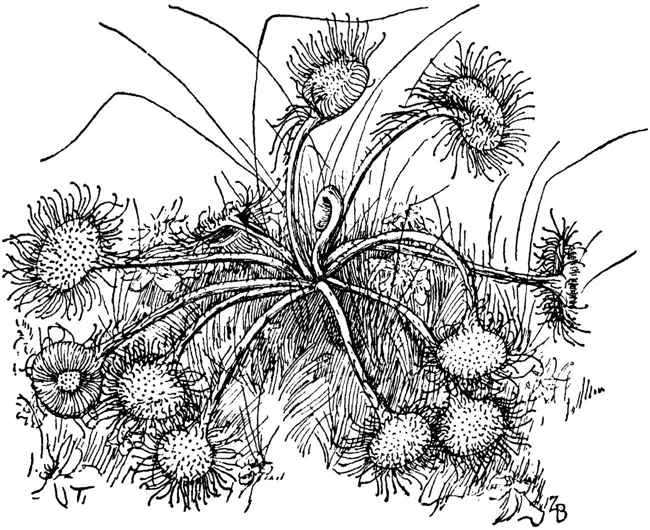


FIG. 89. A sundew (Drosera).

the water crowfoot, for example (Fig. 90), have well-defined palisade and spongy tissues; the submerged leaves, on the other hand, have no palisade tissue, and the intercellular spaces in their spongy tissue are small. The aërial leaves are few-lobed; the submerged leaves are divided into many narrow, thin segments.

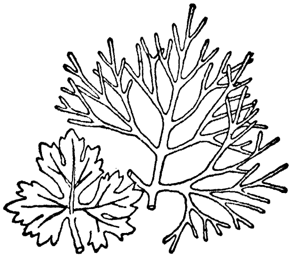


FIG. 90. Aërial (*A*) and submerged (*B*) leaves of a water crowfoot. Modified from Goebel.

Differences may appear also between the leaves first produced by a plant and those formed later. The leaves formed by a young seedling of arbor vitae are needle-shaped (Fig. 91); but after one or more seasons' growth, scale-like appressed leaves develop and ordinarily continue to be formed during the life of the tree. Another example of "juvenile" leaves is seen in the bean, whose first-formed foliage leaves are undivided whereas those formed later are compound.

Leaves of juvenile form are not confined to seedlings; not uncommonly, leaves borne on branches developed from adventitious buds formed in a callus are of the juvenile type. A change in the environment of an older plant, too, may result in the formation of juvenile leaves. The basal (juvenile) leaves of the harebell are rounded, whereas the leaves borne on the upper portion of the stem are long and slender (Fig. 92). An environmental change, such as a marked change in illumination, causes a stoppage of terminal growth, followed by the development of lateral shoots whose basal leaves are rounded.

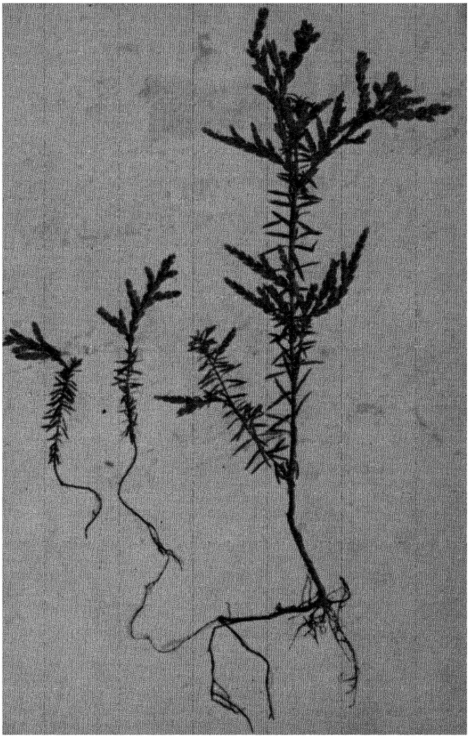


FIG. 91. Seedlings of the arbor vitae bearing leaves of juvenile and adult forms.

66. Fall of Foliage Leaves. In temperate climates the autumnal shedding of leaves by dicotyledonous trees and shrubs is a well-known phenomenon. It is brought about by the development of a special layer of cells (an *abscission layer*, Fig. 93) across the base of each petiole, and sometimes, in a compound leaf, across the base of the stalk of each separate leaflet as well. The cell walls of the abscission layer are thin; the middle layer of each wall becomes dissolved, and finally nearly the whole thickness of the wall is softened and dissolved. The abscission layer does not extend across the vessels and tracheids of the bundle or bundles, whose walls, however, are easily broken by the wind or by the weight of the leaf after the disintegration of the walls of other cells. In some

oaks and other trees, the abscission layer is not well developed in the autumn; dead leaves, therefore, may remain on such trees well into the winter or even into the spring. The cells of the basal part of a petiole immediately below the abscission layer usually develop into a corky tissue which is externally visible on the stem as a *leaf scar*. The fall of a scale leaf, like that of a foliage leaf, is brought about through the formation of an abscission layer.

Many trees and shrubs indigenous to regions without pronounced seasonal changes do not shed all their leaves simultaneously. These plants, exemplified by eucalyptus, oranges, and live oaks, form new leaves and shed old ones continuously throughout the entire year. Such "evergreen" plants are always in foliage.

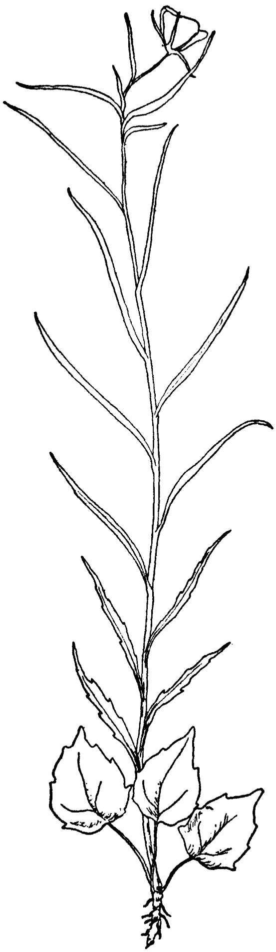


FIG. 92. Harebell (*Campanula rotundifolia*), with leaves of juvenile form at the base, and of adult form on the upright stalk.

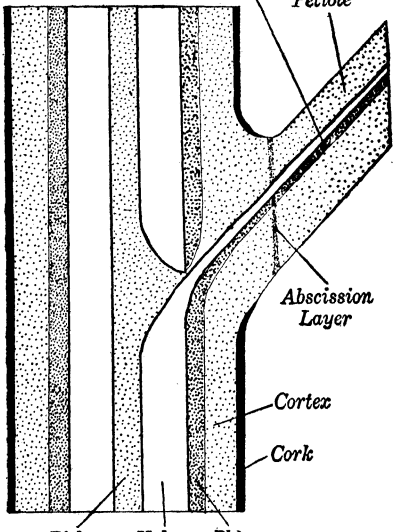


FIG. 93. Diagram showing the attachment of a leaf petiole to the stem, and the position of the abscission layer.

67. Scale Leaves. In many cases a leaf primordium matures into a flattened leaf which is attached to the stem by a broad base, and which carries on little or no food-manufacture. Such a *scale leaf* is usually relatively small, without chloroplasts, and brownish or yellowish in color. Scale leaves about a protected bud prevent mechanical injury of the embryonic parts within. They aid also in checking evaporation from structures within the bud, and so minimize the harmful effects of sudden changes in temperature. The scale leaves of some buds are coated with resin, as in the poplars, and they may be provided with a dense coating of hairs, as are the inner scale leaves of a horse-chestnut bud. Frequently there is no sharp distinction between scale and foliage leaves, and often, as in the lilac, there are all gradations from scale leaves at the outside of a bud to foliage leaves within. After foliage leaves have emerged from the bud, each scale leaf usually falls away. In some buds, like those of the hickory, the inner scale leaves become large and brightly colored before they fall.

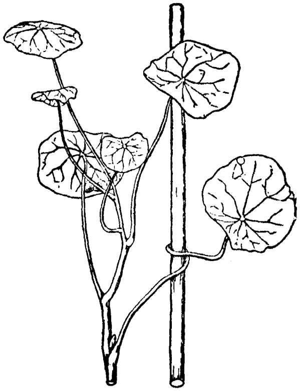


FIG. 94. Leaves of the nasturtium (Tropaeolum), whose petioles function as tendrils.

Scale leaves develop on subterranean, as well as on aërial, stems and branches. The scale leaves surrounding the embryonic region of a subterranean stem or branch constitute a protective sheath which prevents the abrasion of the embryonic region as the stem pushes through the soil.

68. Tendrils and Spines. An entire leaf primordium or a portion only of such a primordium may mature into a *tendril.* A tendril, therefore, may represent a whole leaf or only a part of a leaf. In peas (Fig. 76, *A*) and vetches one or more leaflets toward the terminal end of the leaf are tendrils. In some smilaxes (not including the greenhouse "smilax," which is an asparagus), the stipules are tendrils. In clematis and the nasturtium (Fig. 94) the petioles may function as tendrils, winding about a support and enabling the plant to climb. The term "tendril" is, in fact, applied to any twining portion of a plant which helps to attach the plant to a supporting object. The twining organs of the

grape (Fig. 58) are tendrils, although they are branches rather than leaves.

Spines and thorns, likewise, may be branches, leaves, parts of leaves, or in some cases roots. The common barberry has one to five (typically three) spines at each node (Fig. 95), the spine or group of spines in each case representing a leaf. Some of the spines of cacti (Fig. 96) are leaves and some are branches.

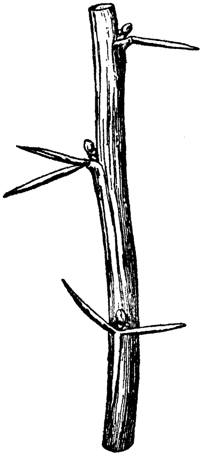


FIG. 95. Winter condition of a stem of the common barberry; the spines are leaves of special form.

SUMMARY

Leaves differ from other vegetative organs in that in general all their cells enlarge and mature simultaneously. Mature leaves may be opposite, whorled, or alternate in arrangement on the stem. A foliage leaf is commonly composed of blade, petiole, and stipules, but some lack petiole, stipules, or both. Leaf blades are either parallel-veined or netted-veined. In the latter case the arrangement of veins may be palmate or pinnate. When marginal lobes of a blade extend to the midrib or to the base of the blade, the leaf is compound. Leaflets of a compound leaf may be pinnately or palmately arranged. Leaflets may themselves be divided.

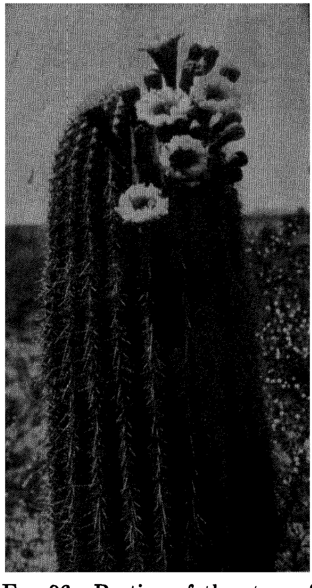


FIG. 96. Portion of the stem of a cactus (*Carnegiea gigantea*), bearing spines and flowers. Photograph by D. T. Macdougal.

Apart from veins, the blade of a dicotyledonous leaf usually consists of the following tissues: upper epidermis, palisade tissue, spongy tissue, lower epidermis. Both lower and upper epidermis may contain stomata. A stoma is a space between two guard cells.

Veins are vascular bundles, continuous with those of the stem,

and consisting of the same primary tissues. Surrounding a vein is a sheath composed of parenchyma and including, in the cases of many large veins, mechanical tissue as well. A petiole contains one or more vascular bundles which connect the vascular bundles of the stem with the veins of the leaf blade.

Structural differences between leaves of various plants are due largely to the proportional amounts present of the various tissues already mentioned. Leaves other than foliage leaves may be scale leaves, tendrils, and spines. The separation of leaf from stem is due to an abscission layer formed at the base of the petiole.

CHAPTER VIII

RELATIONS OF PLANTS TO WATER

69. Importance of Water to Plants. In previous chapters it has been noted that water, together with nutrient substances in solution, is absorbed by roots and is conducted through the vascular tissues of roots, stems, branches, and leaves to all parts of a plant. An ample supply of water is necessary for all the activities of the plant. The importance of water results in part from the fact that it is the liquid in which all or almost all other substances that are to be utilized or are to be moved from cell to cell must be dissolved; and in part from the fact that water is the largest single constituent of protoplasm, which in active cells is ordinarily in a semi-fluid condition. The different organs of a protoplast—such as dense cytoplasm, plastids, and nucleus—differ in the amount of water they contain, but all parts of a living cell must be nearly saturated with water in order to carry on their ordinary functions. The need of a water supply is greatly increased by the fact that water is constantly being lost by evaporation from cells of all aërial parts of a plant, especially from the leaves; and this loss can be compensated only by an intake of water from the soil or from other available source.

As between various organs and tissues, the amount of water present may fluctuate within rather wide limits. In root tips, fruits, and young leaves, the proportion of water may be as high as 90 to 95 per cent. In woody stems the proportion of water is often about 50 per cent; in dormant winter buds 40 to 50 per cent; and in dormant seeds the proportion may be as low as 10 to 15 per cent. The greatest proportion of water is required for activities connected with constructive processes such as those of growth, and the smallest proportion is required for destructive processes such as respiration. Water, however, is necessary to all the physical and chemical changes that occur within the plant.

70. Transpiration. Water evaporates from a free water surface or from a surface containing water; that is, it changes from a liquid state to a vapor and passes into the atmosphere. The evap-

oration of water from the exposed surfaces of a plant is *transpiration*. Since in most familiar plants transpiration is chiefly from the cells of leaves, it is in leaves that this process is most readily studied. On the other hand, the structure of a leaf is best understood if the leaf is considered in its relation to transpiration. The spongy tissue of a leaf is constantly evaporating water into the intercellular spaces, from which the water vapor passes into the outer atmosphere, mainly through the stomata. The epidermis of a leaf allows some water to pass through it, but the amount of water lost to the atmosphere from the epidermis is relatively small in land plants because of the presence in and on their walls of cutin.

That water is lost from the surface of a leaf, and that this loss is mainly through the stomata, may be shown by the following experiment. A geranium leaf is removed from the plant, its lower surface (in which most of the stomata are located) is coated with a layer of wax or vaseline, and the leaf is then laid on a table. Another similar leaf cut at the same time, whose upper surface only is coated, is placed beside the first. The second leaf will wilt much more quickly than the first. The wilting is caused by the loss of turgidity of the cells of the leaf; the loss of turgidity results from a loss of water. The slower wilting of the leaf whose lower surface was coated is due to the fact that most of the water loss was through the stomata. In various cases, from 80 to 97 per cent of the water lost by transpiration passes through stomata, the remainder being lost through the cutinized epidermis.

71. Amount and Rate of Transpiration. Some conception of the extent to which transpiration goes on may be gained by comparing the loss of weight from a pot containing a geranium plant in soil with the loss from a pot of the same size containing soil but no plant. The soil in both pots is well watered at the beginning of the experiment, and both pots are weighed. They are weighed again at the end of 24 hours. The pot containing no plant will be found to have lost some weight because of the evaporation of water from the soil. The other pot will have lost about the same amount in the same way; but the total loss of weight from the pot containing the plant will be much greater. The difference between the losses of weight in the two cases is an approximate measure of the loss by transpiration from the leaves of the plant.

The approximate rate of transpiration may be determined by the use of a potometer (Fig. 97). A cut shoot is fitted into an up-

right tube (*A*); to this tube an empty horizontal tube (*B*) is attached whose free end is bent and immersed in water (*C*). By opening the stop-cock of the vessel *D*, water is driven into tubes *A* and *B*. By removing the end of tube *B* from the water in *C* and allowing the plant to transpire for a short time a bubble of air (*E*) is introduced; the lower end of the tube is then replaced in *C*. Now, as water evaporates from the plant it is replaced by water drawn

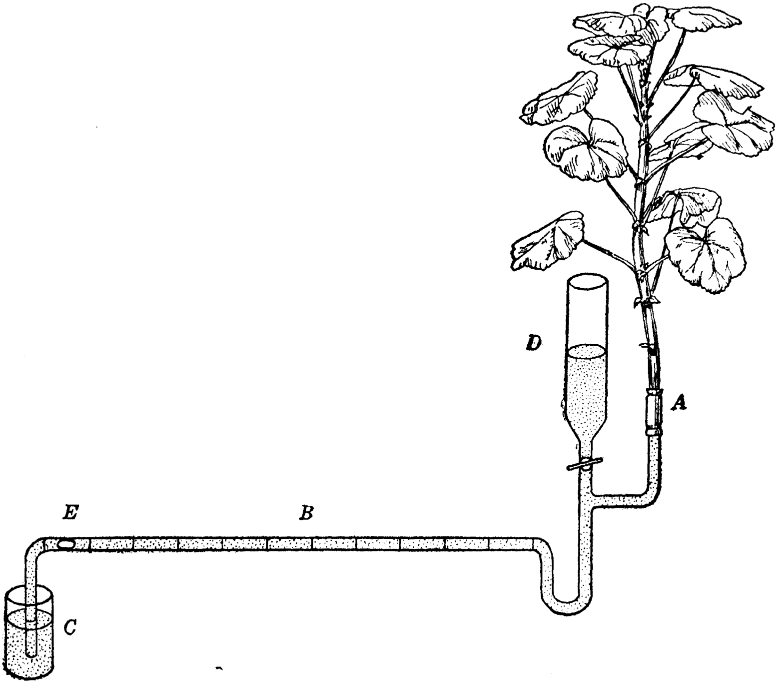


FIG. 97. Potometer, an apparatus used to determine the amount and rate of water-absorption and water-loss by a plant during transpiration.

from tube *B;* the result is a shifting of the bubble *E* toward the plant. By noting the time required for the bubble to move a certain distance, the rate of transpiration may be estimated. If the apparatus is placed under different external conditions, the effects of the environment on transpiration may be studied.

The method just described is not a strictly accurate one for determining the rate of transpiration because it measures the rate at which water is being taken into the plant, and the amount of water transpired may be different from the amount absorbed. The

amount of transpiration and its relation to the amount of water absorbed can be determined by standing the apparatus just described on one pan of a balance, the other pan being weighted to bring the two to the same level. After a half hour or more the pans will no longer be in balance because of the water lost by transpiration. Such a procedure gives some idea both of the amount of water absorbed by the plant and of the amount lost by transpiration.

By far the greater part of the water absorbed by plants is lost by transpiration, and the amount lost is surprisingly large. Under ordinary growing conditions, a square foot of the leaf surface of a sunflower transpires about four ounces of water in the course of 24 hours. In a growing season of 100 days, this would imply a loss of 25 pounds of water per square foot of leaf surface. A single corn plant growing in Kansas has been shown to remove 54 gallons or 1 4/5 barrels of water from the soil in a single season, which is 90 times as much water as is needed by the plant for all purposes except to replace the loss by transpiration. An apple tree 30 years old may lose 250 pounds of water in a day, or 36,000 pounds during the growing season. At this rate an acre of 40 apple trees would transpire 600 tons of water per year.

Experiments show that the amount of water transpired by a plant fluctuates from hour to hour, from day to day, and from season to season. Such fluctuations are due largely to variations in the external conditions, although conditions within the plant and within its individual cells also affect the rate of transpiration. Important among external factors that influence transpiration are the temperature and the humidity of the surrounding air. Winds and air currents affect the process as they affect humidity and temperature. Other things being equal, the drier and warmer the air the more rapid is transpiration. In very moist and cool air transpiration is comparatively slow. Quite apart from the direct effects of the sun's rays upon the temperature of the air, the intensity and quality of light are also important in affecting transpiration. Green leaves and other green parts of a plant absorb a considerable portion of the light rays falling upon them. A small part of the solar energy thus absorbed is used, as will be seen (Chap. IX), in food-manufacture; but in bright light the greater portion is changed to heat and increases the rate of transpiration.

Some of this excess heat vaporizes the water which is then lost

in transpiration. The leaf or other transpiring organ is thus cooled, so that its temperature is kept at or near that of the surrounding air. Transpiration, therefore, tends to regulate the temperature and to prevent excessive heating of the organs of the plant, although this is not the principal significance of transpiration. As will appear later, transpiration is important also as a factor in the transfer to the aërial portions of the plant of water and mineral salts absorbed by the roots.

72. Functions of Stomata and of Intercellular Spaces. The importance of a large leaf surface lies in the fact that it is necessary in the case of a green plant both that a considerable surface be exposed to sunlight, and that a large proportion of its cells have access to certain gases of the air (carbon dioxide and oxygen) which are used by the plant. The large leaves borne by many common plants are adapted to meet these needs; but the presence of such leaves increases the danger of too rapid transpiration.

The aërating system consisting of stomata and intercellular spaces permits, as shown in § 62, the exchange of gases by diffusion between the cells inside and the air outside the leaf. In order that gases may be absorbed by the plant they must be in solution in water. The gases in the intercellular spaces of a leaf pass into solution in the water in the cell walls; the dissolved gases may then diffuse by osmosis into the protoplasts. At the same time, water evaporates from the surfaces of the walls abutting upon the intercellular spaces. The air in these spaces thus tends to become saturated with water vapor. This water vapor can pass to the outside of the leaf only by diffusion through stomata (Fig. 98). The further movement of the water vapor from the outside surface of the leaf depends, among other things, upon the carrying away of the water-laden air by winds and other air movements. Except for the stomata, the leaf is covered by a continuous layer of epidermal cells whose outer walls are in general cutinized and so are relatively impervious to water. Because of the saturation of the air in the intercellular spaces, loss of water from the cells lining these spaces is less rapid than it would be from cells exposing an equal area on the surface of the leaf. The whole arrangement of stomata and intercellular spaces results, therefore, in greatly increasing the area of the leaf that can take in gases from, and give off gases to, the air. The location of the stomata, or of most of them, in the lower surfaces of most leaves results in the loss of

less water than would be lost from the same number of stomata in the upper surfaces, which are more or less exposed to the direct rays of the sun.

Stomatal transpiration consists, therefore, first, in the evaporation of water from the saturated walls of cells lining the intercellular spaces, and second, in the diffusion of the water vapor

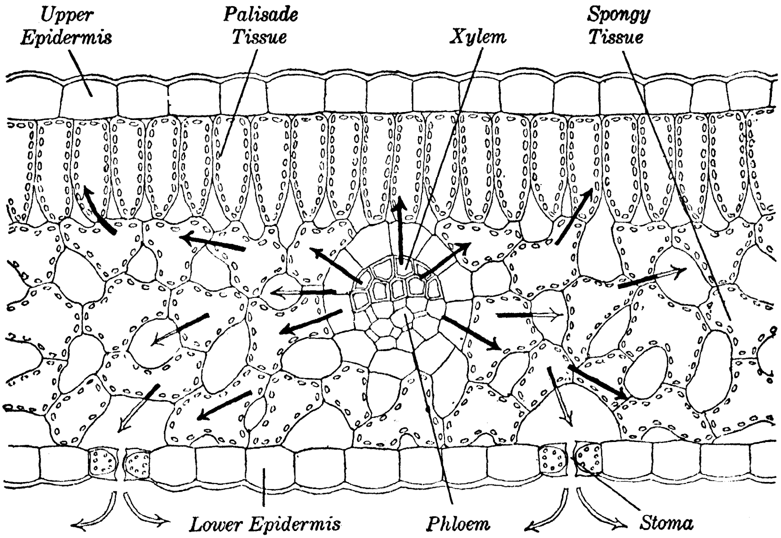


FIG. 98. Diagram showing the paths of movement of water through and out of a leaf. The movement of water in liquid form is indicated by black arrows; that of water in the form of vapor by light arrows.

through stomata. The evaporation of water from the walls of cells adjoining an intercellular space tends to dry out the walls. When this drying begins, the walls of each cell imbibe more water from the included protoplast. Withdrawal of water from the protoplast increases the concentration of substances dissolved in the cell sap, and the cell then tends to draw water by osmosis from neighboring cells that contain proportionally more water. The latter cells in like manner draw from their neighbors, and eventually water is withdrawn from the tracheids and vessels of the veins. These elements of the veins are connected by the tracheids and vessels in the xylem of petiole, stem, and root with the cortex of the root. Thus a continuous stream of water is made possible through root, stem, and branches to the leaf, com-

pensating for the loss of water in the form of vapor from the stomata.

The great number of stomata in the epidermis strongly favors diffusion of water vapor outward and of gases inward. Although stomata occupy but one to two per cent of the surface area of a leaf, diffusion through them can go on almost as readily as though the interior cells were exposed directly to the outside air. The rate of diffusion through an epidermis containing numerous stomata rarely rises to its possible maximum.

73. Guard Cells. One striking characteristic connected with the functioning of stomata in many plants is the ability of the guard cells to undergo changes in turgidity and so to change the sizes of the stomatal openings. The mechanism controlling the movements of guard cells is rather complex, and the responses of guard cells to environmental conditions are also complex. In general, when guard cells are turgid they are arched and the included stoma is wide open, but when they are not turgid they straighten and close or reduce the size of the stoma (Fig. 99). The turgidity or non-turgidity of guard cells is, however, affected by a number of factors, chief among which are the intensity of illumination and the water content of the leaf, especially of its guard cells. In most cases, stomata are open in light and closed in darkness. When water is abundant in the leaves the stomata are usually open; they are usually closed when water is deficient.

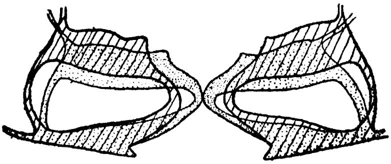


FIG. 99. A stoma in cross section, showing its opening and closing in consequence of changes in the turgidity of the guard cells. The thick walls of the guard cells in the open (turgid) condition are indicated by diagonal shading; in the closed (non-turgid) condition, by stippling. Adapted from Schwendener.

The behavior of guard cells varies in different kinds of plants. In some common plants, such as the potato, cabbage, and beet, stomata are usually open both day and night if the water supply is abundant. On the other hand, in cereals, such as wheat and oats, stomata are always closed at night, and may even close in the daytime if there is a slight deficiency in the water content of the plant. In very many plants the behavior of the stomatal apparatus is intermediate between the extremes just mentioned. In leaves with stomata on both sides, those in the upper surface

open later and for a shorter time than those in the lower surface. Stomata near the tip open later and close earlier than those near the base of a leaf. So many factors affect transpiration, however, that this process is not always most rapid when the stomata are most widely open; and therefore changes in shape of guard cells are not so efficient as might be imagined in regulating transpiration.

74. Means by Which Transpiration Is Checked. When the stomata are completely closed transpiration is stopped. A decrease of 50 to 75 per cent in the diameter of stomata apparently affects transpiration but slightly; a further decrease in diameter, however, results in a perceptible reduction of the rate of transpiration.

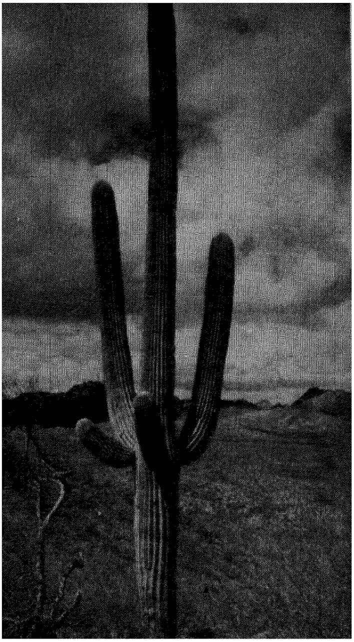


FIG. 100. A cactus (*Carnegeia gigantea*), adapted by its structure to life in a desert. Photograph by D. T. Macdougal.

The shape and size of a leaf markedly affect the amount of water transpired. Some plants of dry regions, like the century plant and the aloes (Fig. 87), have large, thick leaves. Transpiration from such leaves tends to be slow, because even though the area of the leaves may be considerable it is small in proportion to their volume. In some plants, such as certain cacti (Fig. 100), the loss of water is relatively low because the leaves are small or absent, or in some cases are spine-like. Some desert shrubs and trees have leaves during the rainy season but shed them in dry periods. Another extreme is illustrated by plants that, like Elodea, live submerged in water, in which situation transpiration is practically impossible. Such plants ordinarily have very thin leaves. The sunflower, like many common plants, has large leaves which, however, are fairly thick, and are adapted by their structure to limit materially the loss of water by transpiration.

Impregnation of the outer walls of the epidermis with cutin tends to check transpiration. Cutinized walls are characteristic of epidermal cells of leaves and stems that are exposed to the air. In some leaves so much cutin is present that it forms a thin layer (*cuticle*) on the surface. In consequence of the presence of cutin little transpiration takes place from epidermal cells, which otherwise, since they are directly exposed to the air, would lose relatively large amounts of water. A coating of wax, found on such fruits as those of apples, plums, and melons, and even on such leaves and stems as those of the cabbage, also checks epidermal evaporation. Cork acts in the same manner as cutin and wax. The presence of hairs on the surface of a leaf or stem, so conspicuous in the mullein, also may limit transpiration. The location of stomata at the bases of pits, as in the leaves of the pine and of the rubber plant (Fig. 101), has a similar effect.

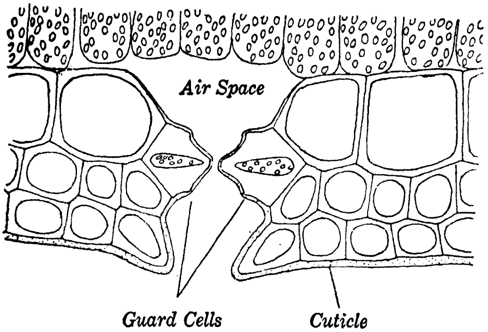


FIG. 101. Cross section of a portion of the lower surface of a leaf of the rubber plant. The heavily cutinized epidermis and the sunken stomata tend to limit transpiration.

Any condition within a protoplast which tends to retain water or to prevent its being imbibed by the walls hinders transpiration. Living matter, because of its imbibing power, always offers a considerable resistance to the removal of water which it contains. The proportion of water in the walls depends, therefore, upon whether or not their imbibing capacity is greater than that of the included protoplast. The degree of saturation of cell walls is influenced also by the osmotic concentration of substances in solution in the cell sap, which may tend to retain water against the imbibitional force of the walls. On the other hand, when a cell is fully turgid, the turgor pressure within its protoplast may be so great as to press out water into and through the wall, so that the outer surface of the wall may become covered with a film of water which then evaporates into an intercellular space. Hence the rate of transpiration may be increased or decreased, regardless of the

size of stomata, by any condition or change in condition of the living matter which affects turgor or the capacity of a cell to take up water (suction tension); by a deficiency of water in the cell owing to excessive transpiration, or by an insufficient supply of water from the soil.

In the cells of thick, fleshy stems or leaves, substances of a mucilaginous nature are often present, which tend to imbibe and retain water. As already mentioned, the leaves of Russian thistle (Fig. 86), the century plant, and the aloe have internal water-storage tissues which can hold large quantities of water. Such plants usually have root systems near the surface of the soil which absorb water quickly after a rain, the water being collected in the stem and leaves. This water is lost very slowly, and some plants with adaptations like those just mentioned can live for months without an external water supply.

Generally speaking, plants native to regions or conditions in which the supply of available water is very limited, such as the semi-deserts of the southwestern United States, possess the most highly developed means of checking transpiration; whereas plants living in habitats permitting access to an abundance of water rarely have special means of hindering transpiration. Plants whose structure fits them to live in deserts and other very dry localities, or elsewhere where water available to the plant is very limited, are *xerophytes;* those fitted for life in water or under extremely moist conditions are *hydrophytes;* and those which stand midway between these two classes, being suited to approximately average conditions with reference to a supply of water, are *mesophytes.* The differences between xerophytes, mesophytes, and hydrophytes illustrate the general rule that living organisms are adapted by their structure and functions to existence in particular types of environment.

75. Water in the Soil. The chief source of soil water is rain. Much of the water falling as rain runs off and some of it evaporates, but some of it enters the soil by gravity between the soil particles. The amount of *gravitational water* which thus enters the soil and its rate of entry depend upon the nature of the soil, the kind and amount of vegetation on the surface, the amount of precipitation, the slope of the land, and the amount of water already in the soil. After a rain some of the water gradually sinks under the influence of gravity until it arrives at the *water table,* the level at and below

which all the spaces in the soil are filled with standing water. As water enters the soil and passes downward, much of it is retained at each level for a time in the form of thin films about the soil particles as well as in the more minute spaces between them. This *capillary water* adheres so closely to the soil particles that it is not influenced by gravity. The films about adjacent soil particles are united, forming a continuous water system which is the source of most of the water absorbed by plants. As water evaporates from the surface of the soil or is absorbed by plants, capillary water moves from adjacent regions where the films are thicker to regions where they are thinner, this movement tending to bring the film-system into equilibrium. Loss of water from the surface of the soil causes an upward movement of capillary water; the effect of this upward movement may extend as far down as the water table, which is then lowered. Lateral movements of capillary water in the soil occur also from regions where water is more abundant to regions where it is less abundant. The mobility of capillary water varies, however, with the character of the soil.

In soils that have lost their capillary water by evaporation, there still remains about each soil particle a thin film of water which is held so firmly that it can be removed only by heating the soil to a relatively high temperature. This *hygroscopic water* adheres so tenaciously to the soil particles that plants are unable to absorb it.

The water in the soil is not pure but contains many dissolved substances, some derived from humus and others from inorganic rock particles. Among these dissolved substances are compounds of nitrogen, sodium, potassium, calcium, magnesium, iron, phosphorus, and sulphur, all of which are significant in the nutrition of plants. The soil water also contains many other solutes that are less important to plants. The actual proportions of the substances in solution in the soil water are usually small, although in some soils relatively large amounts of solutes are present. In some cases much lime is present; "alkali" soils are rich in soluble salts.

76. Air in the Soil. If the spaces in the soil are filled with water, most of the air present is driven out. Ordinarily when water enters the soil it passes downward or evaporates, and the spaces between the soil particles not occupied by water become filled with air. The proportion of carbon dioxide increases and that of oxygen correspondingly decreases with the depth of the soil. The texture

of the soil influences the rate at which oxygen enters and carbon dioxide escapes. Since oxygen is necessary for the respiration and growth of the roots of most plants, an adequate supply of air in the soil is of great importance. In poorly aërated soils not only does the absence of oxygen retard growth, but the concentration of carbon dioxide exerts a toxic action which hinders the growth of roots. The reactions of different plants to the aëration of the soil vary greatly. Most cereal grains and some other plants turn yellow and die when the soil in which they grow is saturated with water for a long period because the presence of water in the spaces between the soil particles excludes the air.

77. Absorption of Water and Solutes. If young roots are removed from the earth, some of the soil adheres to them. This is because the root hairs have grown against and about the soil

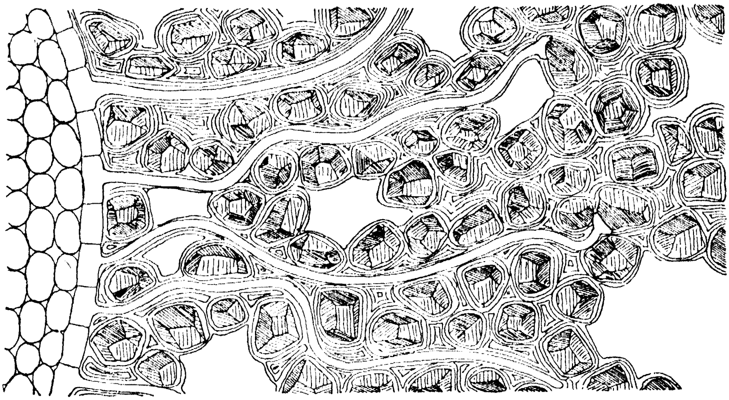


FIG. 102. Diagram showing the relation of root hairs to the soil. The concentric lines about the soil particles show the distribution of water in the soil; the clear areas represent spaces filled with air.

particles, becoming firmly attached to them and so being brought into intimate contact with the water about the particles (Fig. 102) and with organic and inorganic substances, including gases. Roots can absorb much of the capillary water, but can not absorb the thin films of hygroscopic water held about each soil particle. Root hairs greatly increase the absorbing area of roots.

Generally speaking, root hairs are borne on a limited zone 1 to 4 mm. in length near the tip of a root. As a rule, only a limited number of the epidermal cells in this zone bear root hairs; but the

other epidermal cells in the root-hair region, and those in the region immediately back of the root cap, also play a part in absorption. The absorption of water and dissolved substances by roots is determined in part by the laws of diffusion. Water is imbibed by the walls of the root hairs and of the adjacent absorbing cells. In consequence, the water on the outside is continuous through the walls with the water on the inside of the cells, even through the plasma membranes. The liquid in the soil outside each absorbing cell is a dilute solution of very many substances. The cell sap is also a solution, usually on the whole of greater concentration than the soil solution. In consequence of the difference in concentration and of the presence of a differentially permeable plasma membrane, water and its solutes in the soil will tend to diffuse through the cell wall and the plasma membrane into the protoplast. The solutions inside and outside an absorbing cell contain largely different substances; or, if a given substance is present in both solutions, it is likely to be in different concentrations within and without the cell. As a result of such differences an osmotic interchange of great complexity may go on between the cell sap and the soil solution.

The entrance of water into root hairs and adjacent cells depends also upon the suction tension (§ 18) of these cells. Water will enter the protoplast of an absorbing cell of a root and distend the cell wall until the pressures within the cell balance the backward pressure of the elastic wall, when no more water will enter the cell. Under these conditions the cell has lost its suction tension and can absorb no more water whatever the osmotic concentration of the cell sap. If, however, the turgor pressure of the absorbing cell is diminished, its suction tension correspondingly rises.

Water lost by evaporation from the aboveground portions of a plant is replaced by that absorbed by the roots. The loss of water by evaporation tends to increase the concentration of dissolved substances in the cells of the roots including the absorbing cells, and thus to increase the tendency of water to pass into root hairs and adjacent cells, provided these cells are not fully turgid and possess a degree of suction tension. The results of these relations are an entry of water into roots and an absorption from the soil of water and various solutes, many of which are later utilized by the plant; at the same time, other substances dissolved in the cell sap of root hairs and adjacent cells are given off to the soil.

The rate of water-absorption by roots varies with the rate of loss by evaporation of water from the aërial parts of the plant, with the extent of the root system, with the character of the soil and its solutions (some of which may be injurious), with the amount of water in the soil, and with the condition of the absorbing cells. Low temperatures retard absorption. Absorption is influenced also by respiration, which depends upon the presence of oxygen in the soil.

78. Root Pressure. This term designates the pressure exerted by roots under certain conditions in forcing water into and up the

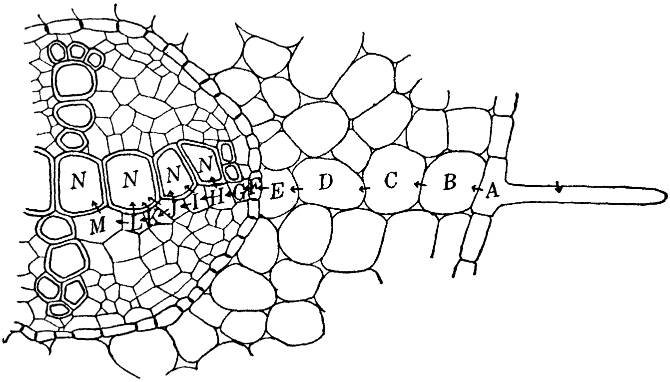


FIG. 103. Diagram showing the path of water-movement from the soil through a root hair and the internal cells into the conducting elements of a root.

stem, as is evidenced by the exudation of water from water pores and from wounds. As has been seen, water can enter root hairs and adjacent epidermal cells when the osmotic concentration of the cell sap is higher than that of the soil solution. The entrance of water into, and its passage through, the cells in the cortex and stele of a root are influenced by the suction tension of these cells as well as by osmotic relations. Water passing through these cells finally reaches the conducting tracts. Only when the suction tension of the cells in the interior of a root is greater than that of the cells farther outward will the interior cells draw water from the outer ones. In such a series of cells as those labeled *A* to *M* in Figure 103, the suction tension is considered as increasing from *A* toward *M*. The cell *M*, having a higher suction tension than *L*, may take water from *L* until *M* becomes so turgid that its

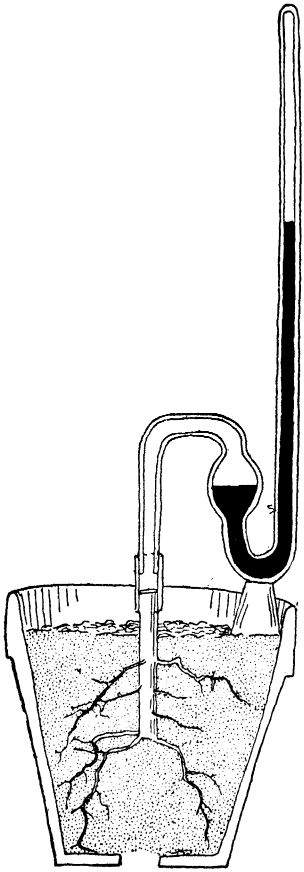


FIG. 104. Experiment demonstrating root pressure. The stem of a potted cutting of a geranium was cut, and its upper part was replaced by a bent closed tube containing mercury. Water exudes from the cut end of the stem, forcing the mercury upward in the tube.

suction pressure is reduced to equal that of *L*. In like manner water may be drawn from cell to cell progressively from *A* toward *M*, providing that the suction tensions of the intermediate cells are progressively higher from *A* toward *M*, as, it is actually observed, may be the case. When the water reaches any cell from *H* to *M*, adjoining a vessel *N*, it may enter the adjacent vessel.

By the process just described, a considerable quantity of water and dissolved substances may enter the cortex of a root and thence pass into the stele, whose tissues are rather rigidly confined by the surrounding endodermis. The cells of the endodermis function to a certain extent in preventing a backward movement of water and of dissolved substances into the cortex. A considerable pressure (root pressure) therefore develops within the stele, which may be sufficient to force water and dissolved substances into the conducting elements of the xylem, where they are free to move upward.

The existence of a root pressure is easily demonstrated by removing the top of a vigorous single-stemmed plant a short distance above the soil and slipping over the cut stump a piece of rubber tubing into which has been inserted a glass tube, arranged with a device to measure the force exerted by root pressure (Fig. 104). Water will exude from the cut surface of the stem and be forced upward in the glass tube. The exudation of water and the rise of the water in the tube result from a pressure in the steles of

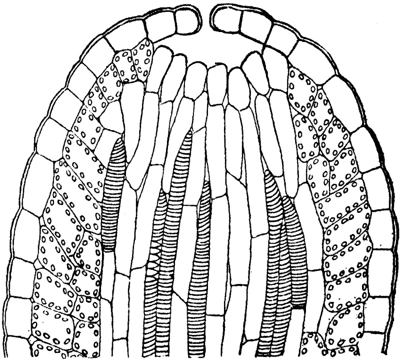


FIG. 105. Water pore at the tip of a leaf of Fuchsia. Water in liquid form exudes from such a pore.

the roots. The magnitude of root pressure and the quantity of water exuded vary in different plants and under different conditions. The exudation from woody stems when cut or wounded is greater than that from herbaceous stems.

79. Loss of Water in Liquid Form. Under certain conditions some plants give off water as a liquid. At the ends of the veins of the leaves of such plants as the cabbage, nasturtium, and Fuchsia are large pores (Fig. 105) which differ from ordinary stomata in that they always remain wide open. Im-

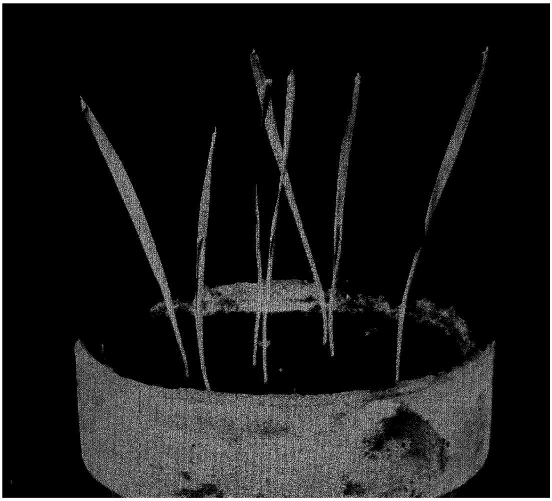


FIG. 106. The exudation of droplets of water from water pores at the tips of the leaves of wheat.

mediately beneath each water pore is a loose tissue devoid of chlorophyll, which is in contact with the end of a vein. When there is an abundant supply of water, and transpiration from such a leaf is limited, water in liquid form escapes through these

pores. In the strawberry and primrose, water pores occur at the tips of the teeth of the leaves. Similar pores are present also at the tips of the leaves of most grasses, such as wheat (Fig. 106) and barley.

The process of exudation of water from water pores may be easily observed if a pot of young, well-watered wheat or barley plants is covered with a bell-jar. In a short time, drops of water appear on the tips of the leaves at the ends of the veins.

Many plants exude liquid water from nectaries (Fig. 107) and other glands. The water thus lost contains substances in solution. The process by which water is given off from glands is not well understood, but it is probably connected with the osmotic activities of particular cells in, or in the neighborhood of, the glands.

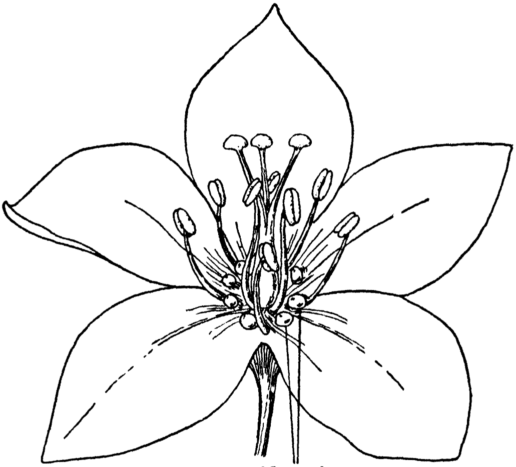


FIG. 107. Flower of the buckwheat, with nectaries at its base.

Plants lose water and solutes from wounds also, and from the cut ends of stems and branches. Large quantities of water may escape during late winter and early spring from such plants as the grape and maple. The sap exuded by wounded stems is never pure water but always, as in the case of the sugar maple, contains solutes. The exudation of water and solutes from wounds is often called *bleeding*. Under conditions favoring absorption of water from the soil, if transpiration is limited, water is forced into and up the xylem of root and stem under considerable pressure and exudes from water pores or wounds. Bleeding is not, however, always due to such root pressure. In the maples, for example, root pressure is very infrequent and bleeding is attributed to the activity of living cells in the neighborhood of the wound.

80. Movement of Water in Stems. When water is absorbed by one part and given off by a distant part of the same plant, a movement of water must take place in the intervening regions. In a very small plant the water transpired may be replaced merely by osmotic movements from cell to cell—the force concerned in these movements being equivalent, not to the osmotic pressure of the cell sap, but to the difference in suction tension between the cells concerned. The conditions in such a plant are very different, however, from those in a sunflower or in a tree. Osmotic movement of water from cell to cell can not possibly suffice to replace the amounts lost by transpiration in these larger plants. The great resistance offered to the passage of water from cell to cell, and the great distances to which water is conducted in large plants, imply the existence of some means for rapid conduction. The long conducting elements of the xylem permit the movement of water and of substances in solution as a mass and at a more rapid rate than would be possible if there were many interposing membranes to be traversed. The movement of water is mainly in the cavities of tracheids and vessels. Water moves in those tracheids and vessels only which are unobstructed and entirely filled with water. The mass of water and solutes moving in the conducting elements of the xylem is the *transpiration stream,* and the movement of this mass is the *sap flow.*

That the path of the transpiration stream is in the xylem may be shown by the following experiment. Take four potted herbaceous plants of a type in whose stem the vascular bundles are separate. From the stem of one plant the pith is removed for a distance through an opening cut in the cortex; from the stem of one the xylem is removed, from another the phloem, and from still another the cortex. If the wounds are protected against drying, as with waxed or oiled paper, the leaves will wilt only in the specimen whose xylem strands have been interrupted.

The path of the transpiration stream may be shown also by cutting off the shoot of a plant which, like Impatiens, has a translucent stem, and placing the shoot in a solution of a dye such as eosin or fuchsin. The general course of the dye can be traced through the stem, the petioles, and the veins of the leaves. Microscopic examination of cross sections of the stem will show that the only elements containing the dye are those of the xylem.

But not all the vessels and tracheids of the xylem necessarily

conduct water. As has been seen (§ 42), the water-conducting elements in trunks of trees become blocked when sapwood changes to heartwood. Hence there can be no movement of water through heartwood. Conducting elements even of the sapwood may become partly or completely filled with gas at certain seasons of the year, in which case there is no conduction through these vessels and tracheids. Such blocking of conducting elements with gases is often so extensive that half of the vessels and tracheids in an annual ring of sapwood are temporarily nonfunctional.

There is a general relation between the volume of transpiration and the amount of conducting tissue developed by a stem. Submerged water plants have relatively few vessels and tracheids. When plants of the same species are grown on land, or when water plants bear branches and leaves above the surface of the water, a proportionally greater amount of xylem is produced.

81. Forces Concerned in Sap Flow. In some trees water is raised to great heights. Such common trees as oaks, maples, and elms often reach heights of 50 to 100 feet. The redwood and some other timber trees of the Pacific Coast states grow to 200 feet or more. The amount of work necessary in lifting enough water to these heights to supply transpiration needs is very great—sufficient not only to raise the water, but also to overcome the resistance encountered in its passage.

The conducting elements, being tubes without protoplasm, can in themselves exert neither suction tension nor any other force that may cause the movement of water. Capillarity is the force which causes water to rise in a slender glass tube, and might therefore be considered responsible for the rise of water entering the very fine tracheids and vessels. However, capillarity operates only where there are free surfaces in open tubes. Within tracheids and vessels which are entirely filled with water no free surfaces are present. Even if they existed, water could not rise in such elements higher than about 30 cm. Therefore, capillarity is entirely inadequate to explain the height to which water is lifted in many trees.

Root pressure plays a minor rôle in bringing about the rise of sap in stems. It has been shown that the parenchymatous cells of the stele force water into tracheids and vessels with which they are in close contact (Fig. 103). Root pressure, however, is not of

prime importance in forcing water upward in a stem, since it is least when transpiration and water movement in the stem are most rapid.

The force which chiefly accounts for the ascent of sap is that exerted by the transpiring cells of the leaves. As has been seen, a living cell of a leaf, because of the presence of dissolved substances in its cell sap, exerts a suction tension by virtue of which it tends to draw in water. As water evaporates from the leaf the suction tension of the transpiring cells rises; as a result, they take water from the adjoining cells within the leaf, and these in turn draw it from still more deeply lying cells. Ultimately the suction force is applied to the columns of water in the tracheids and vessels of the veins of the leaf, which are connected through the petiole with xylem elements in the branch; the latter are connected with xylem elements in the stem or trunk, and these in their turn with elements of the xylem in the root. In effect, there are continuous columns of water in the xylem elements of root, stem, branch, and leaf; and upon the upper ends of these columns the force generated in the leaf cells exerts an upward pull.

The suction force so exerted by the cells of leaves is found to run from 5 to 10 atmospheres, and in some cases very much higher. Since a suction force of one atmosphere can raise a column of water about 30 feet, it is evident that the force exerted by leaf cells is sufficient to raise water to the height of the tallest trees if that force is efficiently applied, and if the columns of water in the conducting tracts are not broken.

82. Tensile Strength of Water. Contrary to what would be imagined from ordinary experience with water, experiment shows that a column of water has great tensile strength. When the tensile strength of a bar of metal is tested, the force required to break it is considered equal to the force of cohesion of its molecules. In liquids the molecules are more mobile and their cohesive force is more difficult to measure. However, by means of proper apparatus it is shown that the molecules of water enclosed in a tube tend very strongly, like those of a metal bar, to cohere. Because of the cohesion of the water columns in the xylem, the pull exerted by the leaf cells lifts the columns. In a tree 100 feet tall, the effect of the pull is felt for 100 feet plus the distance to the most remote root. The pull upon the water columns is continuous so long as transpiration is active. If intake of water by the roots is ample, a stream of

water is kept flowing continuously upward through the xylem to the leaves.

83. The Water Balance in Plants. By far the greater part of the water absorbed from the soil by a plant is lost as water vapor. From what has been said it is evident that the movement of water in the plant is affected by the rate and amount of absorption of water from the soil and by the rate and amount of transpiration. Any condition in the soil, such as its proportional water content or the concentration of solutes in the soil water, usually affects the rate of transpiration. However, transpiration and absorption are not always directly proportional, and water may be transpired by a plant more rapidly than it is absorbed by the roots. Conversely, water may be absorbed more rapidly than it is lost by transpiration.

When water is lost more rapidly than it is absorbed, the water balance is changed and a deficit exists. A considerable water deficit is likely, therefore, to exist in a plant during periods of active transpiration. About midday on bright, sunny days many plants lose considerably more water than they can absorb; the resultant water deficit in a sunflower plant may reach 28 per cent of its maximum water content. Fluctuations in the water content of leaves of common plants (such as wheat, sugar beet, or pumpkin) may under some climatic conditions be as great as 20 per cent. Even in plants with an extensive water supply and whose transpiration is limited, a daily deficit may occur. When transpiration is excessive, as on very warm, dry days, a plant can not make up the water deficit during the night, so that it may still have a deficit the next morning.

With continued drought and consequent lack of water in the soil, the daily water deficit in the plant increases. The loss of turgidity in the cells leads to a loss of rigidity, and the leaves and young stem and branch tips droop or *wilt*, although elsewhere in the plant the water content may be relatively high. Such wilting often occurs at midday when transpiration is active; but ordinarily toward evening, when transpiration decreases, the water deficit is restored and the plant recovers its rigidity. This occurs even without any appreciable absorption of water from the soil, the water already in the plant being redistributed. Under certain conditions the water content may become so depleted that the plant recovers from a wilted condition only with difficulty if at all. Permanent wilting occurs when soil water is no longer available

to the plant, and the living cells of all organs, including root hairs, gradually lose their turgor. After permanent wilting the plant absorbs water, if at all, very slowly from moist soil, and not until new root hairs are formed. In most plants, when the leaves have wilted, the guard cells lose their turgidity and close the stomata, thus interfering with an exchange of gases between the inside and the outside of the leaf. During permanent wilting, structures such as chloroplasts are injured, the result being usually permanently harmful to the plant.

In some plants special water-storage tissues or regions, occurring in certain leaves and in stems adapted to hold water like those of cacti, may contain sufficient water for considerable growth and transpiration; but unless water is supplied from other sources, even plants with such structures eventually perish. Some plants growing in dry regions, because of their power of storing and retaining water, can live for months without an external supply.

CHAPTER IX

THE MANUFACTURE OF FOODS

84. Plastids: Chloroplasts. An important part of the work of food-manufacture in living cells is carried on by bodies of a class known as *plastids*. The plastids of mature cells, at least in the higher plants, are developed from the chondriosomes (§ 21) of embryonic cells. As an embryonic cell becomes mature, some (by no means all) of its chondriosomes enlarge and take on the characteristics of plastids. Those plastids which are green in color are chloroplasts (Fig. 108). Certain types of plastids other than chloroplasts will be discussed later.

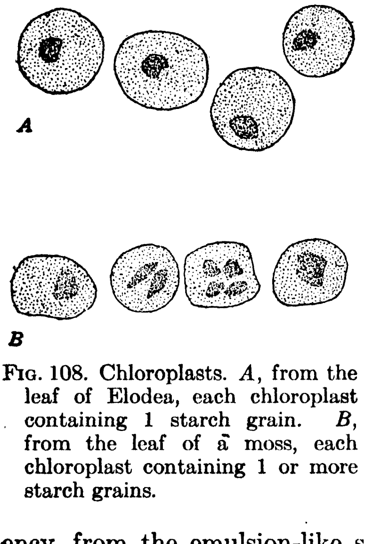


FIG. 108. Chloroplasts. *A*, from the leaf of Elodea, each chloroplast containing 1 starch grain. *B*, from the leaf of a moss, each chloroplast containing 1 or more starch grains.

The chloroplasts of most of the larger land plants are usually small and spheroidal, ellipsoidal, or (if crowded) polyhedral; the number in a cell varies from one to many. In green food-manufacturing tissues, such as the palisade tissue of a leaf, many chloroplasts are present in each cell. A chloroplast appears to be of a spongy nature; its framework is not fundamentally different, except for its firmer consistency, from the emulsion-like structure of the surrounding dense cytoplasm. A continuous sheath of dense cytoplasm immediately surrounds the chloroplast. The center of the body is less dense, or vacuolate, and may contain a single large vacuole (Fig. 109).

85. Chlorophyll. The green color of chloroplasts is due to the presence of two green pigments, which together are called *chlorophyll*. Little is known as to just how these pigments are held in a chloroplast. Apparently they exist in a finely divided state in the peripheral framework. That the pigments are distinct from the

chloroplast is shown by killing a leaf in boiling water and then immersing it for some time in alcohol. The alcohol becomes green, and when the leaf is removed it is found to be colorless, the chlorophyll having been dissolved in the alcohol. Microscopic examination discloses the now colorless chloroplasts still present in the cells of the leaf. Chlorophyll is a mixture of chlorophyll *a*, which is blue-green, and chlorophyll *b*, which is yellow-green. These pigments ordinarily occur in the proportion of about 72 per cent of chlorophyll *a* to 28 per cent of chlorophyll *b*.

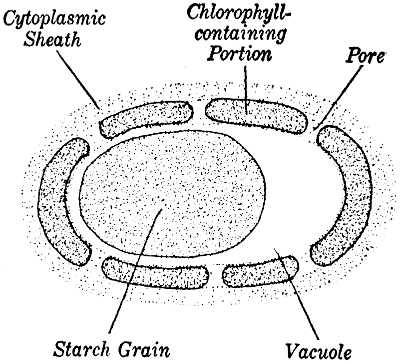


FIG. 109. Diagram of a chloroplast (in section), showing distribution of chlorophyll. Modified from Zirkle.

Chlorophyll and the other pigments contained in chloroplasts are insoluble in water and in the cell sap, but are soluble in alcohol, ether, acetone, and various other liquids. The extract obtained from a leaf includes, besides chlorophyll *a* and *b*, certain yellow pigments. If an alcoholic leaf extract is diluted with water and then benzol is added, the benzol soon rises to the top of the mixture as a sharply defined, deep green layer, while the water and alcohol below show a pale yellow or straw color. The green color at the top is due to the two chlorophylls; the yellow color at the bottom to the yellow pigments. Of the yellow pigments occurring in plastids, the best known are *carotin*, usually deep yellow or orange in color, and *xanthophyll*, which is light yellow or lemon-colored. The presence of carotin and xanthophyll affects the color of leaves, which is yellow-green rather than pure green.

When plants are grown in darkness, the plastids lack chlorophyll but contain yellow pigments. In some plants growing in the light, chlorophyll fails to develop in the plastids of certain cells. In the silver-leaf geranium chlorophyll-development is limited to certain areas of the leaf blade, other areas being white or yellowish white (Fig. 113, *A*). Sometimes a whole leaf or branch is entirely devoid of chlorophyll. The plastids in the lighter portions of such a plant contain carotin and xanthophyll, whereas in the plastids of the green areas chlorophyll also is present.

86. Formation of Chlorophyll. Except in some very simple plants, chlorophyll occurs only in definitely organized chloroplasts. It is manufactured by the living matter of the cell, apparently by that portion of the cytoplasm which constitutes the chloroplasts. The production of chlorophyll is dependent upon various factors both within and without the plant.

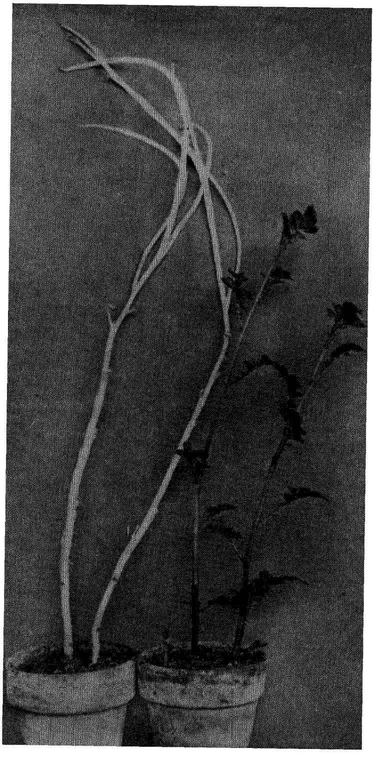


FIG. 110. Potato shoots grown in darkness (left) and in the light (right).

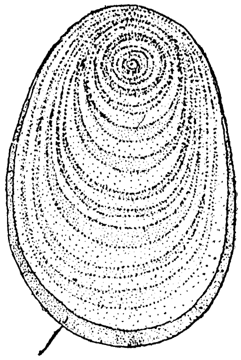
Light is one of the factors necessary to chlorophyll-formation, which occurs in the presence of light of most wave lengths (that is, of most colors). It is much more affected by the intensity than by the wave length of light, although for light of equal energy values the red rays are more effective than the green, and the green are more effective than the blue. A medium intensity of light is most favorable for the production of chlorophyll.

The chlorophyll formed within a chloroplast is not stable but breaks down within a relatively short period. This fact is not evident in plants growing in the light, since the disintegrating chlorophyll is being continually replaced by that which is newly formed. It becomes evident, however, when green plants are placed in darkness, since the plant is then unable to form new chlorophyll. In sufficiently intense light, although its formation and decomposition occur simultaneously, chlorophyll is destroyed faster than it is formed, whereas in diffuse light the reverse is true.

Plant parts which would be green if grown in light, when grown in darkness do not form chlorophyll and hence are whitish or pale yellow. Such parts contain some of the yellow pigments, especially

carotin and xanthophyll. Plants grown in darkness, as compared with those grown in light, also frequently show marked differences in the forms of their aërial organs; these differences, together with the absence of green color, are summed up under the term "etiolation." Etiolated shoots of the potato (Fig. 110) or of the bean have long, slender internodes, elongated petioles, and small leaf blades. Etiolated shoots of wheat, barley, or corn have greatly elongated leaves, and sometimes the internodes are unusually long.

Chlorophyll is formed only within a relatively narrow range of temperature. In etiolated plants brought into light, chlorophyll is produced most rapidly between 18° and 30° C. A chlorophyll molecule, whether of chlorophyll *a* or *b*, contains the elements carbon, hydrogen, oxygen, nitrogen, and magnesium. The presence of each of these elements, therefore, in appropriate compounds is necessary to the production of chlorophyll. Carbohydrates also must be present if chlorophyll is to be formed. Although iron is not a constituent of the chlorophyll molecule, its presence is necessary for chlorophyll-formation, and plants grown in the absence of iron are yellowish. Variations in the amounts of calcium, sulphur, potassium, manganese, and phosphorus present, as well as the absence of iron, also may cause a yellowing, although none of these elements enters into the composition of chlorophyll. The presence of a large number of elements and compounds, therefore, favors chlorophyll-formation; on the other hand, the presence in too great quantities of some substances, one of which is common salt, impedes the process.



Leucoplast

FIG. 111. Starch grain formed in a leucoplast; from a potato tuber.

87. Plastids Other than Chloroplasts. *Leucoplasts* are similar in appearance to chloroplasts, except that they contain no pigments. Lacking chlorophyll, they can not carry on photosynthesis; they can, however, like chloroplasts, manufacture starch from sugars (Fig. 111). They occur chiefly in parts of plants not exposed to light, in which starch is stored; such as the cortices of aërial stems and various tissues of underground stems and roots. They are particularly abundant in many seeds and fruits, as in

those of the cereal grains. Not infrequently, if such an underground organ as a young potato tuber is exposed to light, chlorophyll appears in the leucoplasts which thereby become chloroplasts. In this case, whether a particular plastid is to be a leucoplast or a chloroplast is determined by external conditions, particularly by the presence or absence of light. Some colorless plastids, however, like those in the marginal cells of the silver-leaf geranium, can not under any conditions become chloroplasts.

Chromoplasts lack chlorophyll but contain some of the other pigments, especially carotin and xanthophyll. While carotin and xanthophyll are typically yellow or orange, they may vary in depth of color to orange-red, brick red, or reddish brown. These colors occurring in flowers, fruits, and various other organs are due usually to the presence of chromoplasts. Chromoplasts are more variable in form than are either chloroplasts or leucoplasts. In the cells of some of the floral parts of the nasturtium (Fig. 112), the chromoplasts are angular and orange-red. Those in the fruit of the climbing bitter-sweet are crescent-shaped and reddish brown. Other fruits whose colors are due to the presence of chromoplasts are those of the tomato, rose, and red pepper.

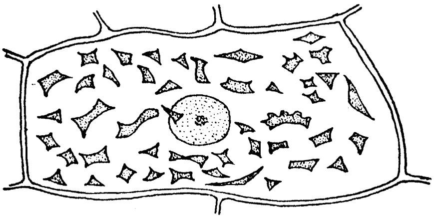


FIG. 112. Chromoplasts in a cell of a flower of nasturtium. After Strasburger.

Elaioplasts, whose particular function seems to be the storage of fats, occur in some plants.

88. Photosynthesis. As has been seen, elements unite to form simple compounds; these may be combined into more complex substances. One particular process which is fundamental to the activities and continued existence of plants is the combination of carbon dioxide and water into a sugar. This combination is brought about only in the chlorophyll-containing cells of living plants, and only in the presence of light. Since it involves a putting together (*synthesis*) of simple substances into one that is more complex, and since light is essential, the process of thus combining carbon dioxide and water is called *photosynthesis*.

Photosynthesis is a complex process whose early stages are not certainly known. Carbon dioxide and water are decomposed, and

the products of their decomposition are recombined. In the course of these changes oxygen is given off. The first product of photosynthesis that can be detected is usually a sugar, most commonly glucose ($C_6H_{12}O_6$). It is probable that a relatively simple compound, such as formaldehyde (CH_2O), is first produced from carbon dioxide (CO_2) and water (H_2O), and that molecules of this substance are then combined to form glucose. Whatever the intermediate stages, the end result of photosynthesis may be expressed by a formula like the following:

$$6\ CO_2 + 6\ H_2O = C_6H_{12}O_6 + 6\ O_2.$$

In any event, the substances formed in photosynthesis are carbohydrates, the basic substances from which all other organic compounds in animal and plant bodies are produced. Glucose, like other sugars, is a food that may itself be used by the cell which formed it, in the building up of other compounds; or it may have the effect of maintaining or increasing the osmotic concentration of the cell contents. Being readily soluble in the liquids of a plant, glucose may diffuse from cell to cell in solution. Its diffusion is slow, however, and when photosynthetic activity is considerable, glucose (or another sugar) is formed more rapidly than it diffuses away from the cell in which it is made.

An accumulation of large quantities of a sugar greatly increases the osmotic concentration within a cell and thus interferes with various activities of the living matter. This difficulty is obviated in many plant cells by a change of glucose into another carbohydrate which is not readily soluble in water. The insoluble carbohydrate into which sugars are most commonly converted in plant cells is *starch.*

Not only is the sugar produced by photosynthesis necessary to the plant that manufactures it; sugars, or substances derived from sugars, are indispensable to those organisms, plant or animal, which lack chlorophyll, with the exception of a few groups of bacteria which can live independently of the compounds formed by green plants. Apart from these bacteria, the existence of all living organisms is dependent upon the occurrence of photosynthesis in plant cells containing chlorophyll.

89. Conditions Essential to Photosynthesis. Photosynthesis is possible only at a suitable temperature and in the presence of living matter, chlorophyll, water, carbon dioxide, and light. That

the process is dependent upon the presence of chlorophyll may be shown in the following way. If a leaf of the silver-leaf geranium, already referred to, after being exposed to the light for

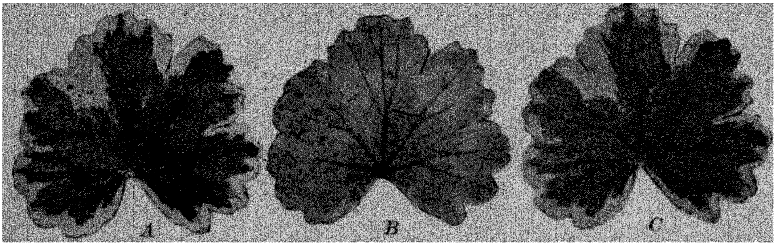


FIG. 113. Experiment illustrating the necessity of the presence of chlorophyll for photosynthesis. *A*, fresh leaf of the silver-leaf geranium. *B*, the same leaf with the chlorophyll extracted. *C*, the starch-containing portion of the leaf has turned dark blue after treatment with iodine. Note that the starch pattern in *C* corresponds with the chlorophyll pattern in *A*.

an hour or more, is killed with boiling water, the chlorophyll extracted with alcohol, and the leaf placed in a solution of iodine, the portions which formerly contained chlorophyll turn dark blue, but those which lacked chlorophyll remain white or become yellowish (Fig. 113, *C*). Since starch in contact with iodine turns blue, the experiment shows that starch was formed only where chlorophyll was present. Another method of demonstrating the same fact consists in planting specially selected kernels of corn, some of which will produce green and others white plants (Fig. 114). For the first few days plants of both types grow with equal rapidity, but after the food reserves of the kernels have been used by the seedlings the green plants will continue to grow while the white plants will die. Because of the presence of chlorophyll,

FIG. 114. Green and white corn plants of the same age. Note the greater growth of the plant at the right, which contains chlorophyll.

the green plants can manufacture their own food; the white plants, having no chlorophyll, can not.

That carbon dioxide is necessary for photosynthesis, and that this atmospheric gas is used in sugar-manufacture, can be demonstrated by selecting two vigorous Coleus or nasturtium plants and placing them in the dark until the iodine test no longer discloses the presence of starch in their leaves. One of these plants is then placed under a transparent glass bell-jar (Fig. 115); the air that enters the bell-jar must pass over some substance, such as soda-lime, which absorbs the carbon dioxide but not the other atmospheric gases. Within the bell-jar is placed a dish containing a solution of soda-lime to absorb any carbon dioxide there present. The other plant is placed in a bell-jar similarly equipped, except that particles of brick of the same size are substituted for those of the soda-lime, and that water replaces the soda-lime solution within the bell-jar. The brick does not absorb carbon dioxide, so that the plant can obtain this gas as well as the other atmospheric gases. If, after several hours' exposure to sunlight, leaves from each plant are tested with iodine, those from the plant in the first bell-jar remain colorless but those from the second turn blue, showing that sugar, and later starch, were formed only when carbon dioxide was available to the plant.

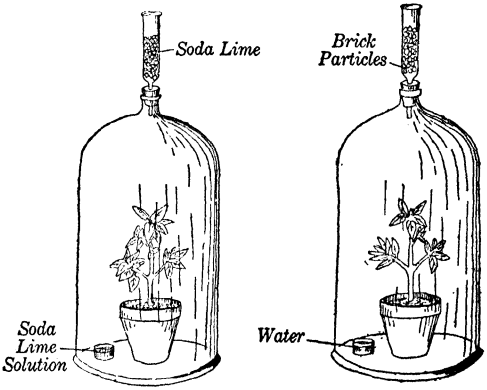


FIG. 115. Experiment showing the necessity of carbon dioxide for photosynthesis. For explanation see § 89.

The amount of carbon dioxide in the air is only about 3 parts in 10,000 (0.03%). In some localities, as in the neighborhood of cities and factories, the proportion may be slightly higher. Although a large amount of leaf surface which can absorb carbon dioxide is exposed to the atmosphere, the ordinary supply of this gas is often insufficient for the maximum possible amount of photosynthesis. When the supply of carbon dioxide is artificially in-

creased to 1 per cent, photosynthesis becomes correspondingly more rapid. Since carbon dioxide enters a leaf through its stomata, the number and distribution of stomata and the extent to which they are open affects the entrance of the gas into the leaf and therefore affects the rate of photosynthesis. That this is true can be shown by coating with vaseline a portion of the surface of a leaf having stomata only on its lower side. This blocks the stomata and so prevents the entrance of carbon dioxide. If the leaf is tested with iodine after sufficient exposure to light, it will be found that no starch is present in that portion of the leaf whose stomata were blocked.

FIG. 116. *A*, light screen attached to a leaf. *B*, leaf after exposure to light under a light screen. The dark portions of the leaf show the distribution of starch, as demonstrated by treatment with iodine.

The necessity of light for photosynthesis can be shown by covering the whole or a part of the surface of a green leaf with a screen made of some opaque substance, such as tinfoil or black paper (Fig. 116, *A*), so arranged that it will exclude the light but will not interfere with transpiration or with the exchange of gases between the inside and the outside of the leaf. It is best to select a leaf on a vigorously growing plant which has been kept in the dark for one or more days, because leaves on such a plant do not ordinarily contain starch. If, after adjusting the light screen, the leaf is exposed to the sun for an hour or more, then removed from the plant and tested, it is found that the portions exposed to the light contain starch (Fig. 116, *B*), but that no starch is present in the portion from which light was excluded. This experiment shows, not that light is concerned directly in the formation of starch, but that light is necessary to the manufacture of a sugar which, after its formation, is converted into starch.

Photosynthesis proceeds best in sunlight of appropriate intensity, but it goes on in greenhouses in the presence of a suitable kind of electric light. For many plants ordinary direct sunlight is too

intense, and photosynthesis is most rapid in such plants in strong diffuse light.

90. Energy and the Function of Chlorophyll. In the study of photosynthesis it is relatively easy to determine, at least in outline, the *material* changes that are involved in the combination of carbon dioxide and water into such a carbohydrate as glucose. Intimately connected with these material changes are changes that involve *energy.* Every substance contains, or possesses, a certain quantity of energy. Some of the energy possessed by a substance may more or less readily be changed into another form. For example, chemical energy is changed in the process of combustion (burning) to heat energy. Energy which may thus fairly readily be changed is *available* energy. Great amounts of energy are locked up, as it were, in the atoms of any substance and are not available by any ordinary means. The available energy content of carbon dioxide and that of water are relatively low; on the other hand, the available energy content of glucose or of any other carbohydrate is relatively high. When, therefore, through the agency of chlorophyll, carbon dioxide and water have been combined to form a sugar, the newly formed sugar possesses a stock of energy which was not present in the water and carbon dioxide. The energy that has thus been stored in the sugar was obtained from the sunlight by the plant cell through the agency of chlorophyll. In the process, light energy was changed into chemical energy. The function of chlorophyll in this change is comparable to the function of an automobile motor which changes the chemical energy of gasoline into the mechanical energy that moves the car.

The energy thus utilized and transformed by the agency of chlorophyll must first be taken by the chlorophyll from the sunlight. Part of the energy of the light which penetrates any substance is absorbed by that substance; no effect can be produced by light unless it is absorbed. An important characteristic of chlorophyll is its capacity to absorb a considerable fraction of the energy of the light falling upon it and to transform a portion of this energy into chemical energy.

Sunlight is composed of different kinds of light. When a beam of light passes through a prism, it is split into its component parts, the visible ones of which produce on the human eye the sensations of the colors red, orange, yellow, green, blue, and violet.

The splitting of the beam is due to the different degrees to which its component rays are deflected by the prism. The band of varied colors thus produced is the *visible spectrum.* If an alcoholic extract of chlorophyll from a leaf is placed in the path of a beam of sunlight, and the beam after passing through the extract is dispersed by a prism, the spectrum appears interrupted by several

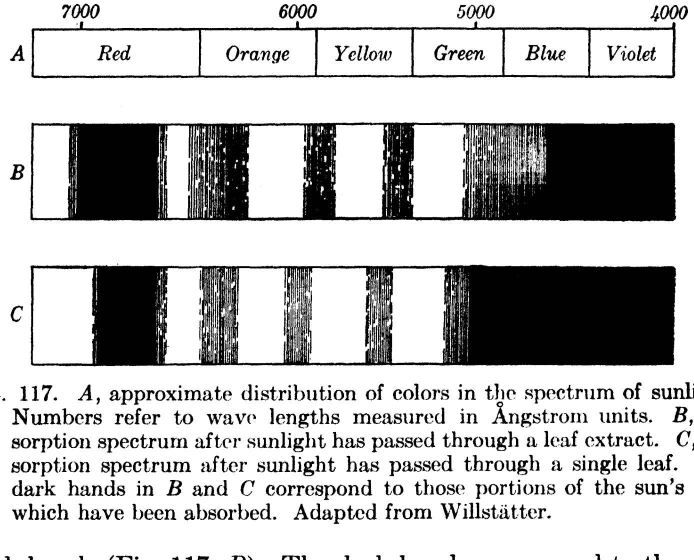


FIG. 117. *A*, approximate distribution of colors in the spectrum of sunlight. Numbers refer to wave lengths measured in Ångstrom units. *B*, absorption spectrum after sunlight has passed through a leaf extract. *C*, absorption spectrum after sunlight has passed through a single leaf. The dark hands in *B* and *C* correspond to those portions of the sun's rays which have been absorbed. Adapted from Willstätter.

dark bands (Fig. 117, *B*). The dark bands correspond to the portions of the beam of light which have been absorbed by the extract. Some of the bands located toward the red end of the spectrum, and some toward the violet end, are caused by the absorption of the corresponding rays of light by chlorophyll *a* and chlorophyll *b*. Two or three bands toward the violet end of the spectrum are caused by the absorption of light by carotin and xanthophyll. Experiments show that the light of particular wave lengths which is absorbed by chlorophyll is the energy used in photosynthesis. Plants which lack chlorophyll, with the possible exception of certain bacteria already mentioned, can not transform the energy of sunlight into the chemical energy used in photosynthesis. In strong direct sunlight, the energy absorbed by chlorophyll from the red portion of the spectrum is most efficient in photosynthesis; in diffuse light those rays toward the blue end of the spectrum are more important in the process. Only about 0.5 to 3 per cent of

the light energy falling upon a leaf in direct sunlight is used in photosynthesis; some of the light is reflected, some is transmitted, and a considerable proportion of that which is absorbed is transformed into heat; the heat in turn is used to evaporate the water lost in transpiration.

It is evident from the preceding discussion that the process of photosynthesis is affected by both external and internal conditions. The factors chiefly affecting it are the carbon dioxide content of the air, temperature, light, and the amount of chlorophyll present.

Any substance that possesses energy which is available to a plant or animal is a *food*. Among the substances that may serve as foods are glucose, other sugars, and other carbohydrates into which sugars may be converted. Since light energy has been transformed into the chemical energy of carbohydrates, these are reservoirs of the energy of sunlight. It is only in cells containing chlorophyll that this transformation of the energy of sunlight can occur.

91. Carbohydrates Other than Glucose. Glucose may be transformed, in the cell in which it is produced or in another cell to which it has passed, into any one of a considerable number of sugars. Among these are sugars having the same formula as glucose ($C_6H_{12}O_6$), but in whose molecules the atoms are differently arranged. Some sugars are simpler than glucose, having 5 carbon atoms in each molecule instead of 6. Among those more complex than glucose are cane sugar ($C_{12}H_{22}O_{11}$), found in the sugar beet, sugar cane, and sugar maple; and malt sugar, having the same formula as cane sugar, which is present in sprouted barley.

It has been seen that another carbohydrate into which glucose may be changed is starch. In a cell in which photosynthesis is going on, starch is often deposited in the form of a small grain or of several small grains within each chloroplast (Fig. 108). The amount of starch formed in such a cell is approximately proportional to the rate at which photosynthesis is proceeding. In the production of starch it is thought that the equivalent of a molecule of water (H_2O) is extracted from each molecule of glucose, so that a new unit of the composition $C_6H_{10}O_5$, instead of $C_6H_{12}O_6$, is formed, and that many such units are combined to form a molecule of starch. The formula of starch, therefore, is written $(C_6H_{10}O_5)_n$, the n indicating an indefinite but large number of units.

Another carbohydrate produced by the transformation of

sugars is *cellulose,* which frequently forms a large proportion of the substance of cell walls and which exists in an almost pure state in cotton fibers. Cellulose is deposited in the cells of some plants as a reserve food. Other carbohydrate foods produced by certain plants are *glycogen* and *inulin.*

92. Fats. Some of the carbohydrates seem to serve as the chief building materials for *fats,* examples of which are olive oil, cottonseed oil, and linseed oil. Many seeds and fruits, as for instance the castor bean, soybean, peanut, and olive, are particularly rich in fats. Although composed of the same elements as carbohydrates (carbon, hydrogen, and oxygen), a fat molecule differs markedly in its organization from a carbohydrate molecule, one important difference being its lesser proportion of oxygen. As an illustration, olein, the fat most largely present in olive oil, has the formula $C_{57}H_{104}O_6$. The energy content of fats is higher in proportion to their volume than is that of carbohydrates, and consequently fats are foods by means of which a large amount of available energy may be stored in a very limited space. Fats, like starch, are practically insoluble in the cell sap.

93. Proteins. Carbohydrates and some nitrogen-containing compounds are the chief sources for the synthesis of *proteins.* Proteins constitute an essential part of the living matter of all plant and animal cells. They are also often present as reserve foods, being especially abundant in peas, beans, and similar seeds, and in the outer portions of the kernels of wheat, oats, and corn.

All proteins contain carbon, hydrogen, oxygen, and nitrogen; many contain also small proportions of sulphur and phosphorus. The nitrogen, sulphur, and phosphorus are derived from relatively simple compounds, such as nitrates, sulphates, and phosphates, which most of the familiar green plants obtain in solution from the soil. Phosphorus-containing proteins are particularly characteristic of nuclei, although some cytoplasmic proteins also contain this element.

Proteins are extremely complex, their molecules being composed of very large numbers of atoms. For example, the formula of gliadin, found in the wheat kernel, is $C_{685}H_{1068}O_{211}N_{196}S_5$. Although formulas of this nature have been determined for a few proteins, the *exact* chemical constitution, that is, the arrangement of the atoms in the molecule, is not known for any protein that occurs in living cells. However, much has been learned regarding

the simpler compounds (*amino-acids*) of which a protein molecule is composed; and a considerable number of these simpler compounds have been artificially combined into substances that may be considered comparatively simple proteins.

Proteins, as well as many other components of living matter, occur in the *colloidal* state—a state marked by the distribution of the substances in question in a more or less finely divided condition through a continuous medium. This medium, in protoplasm, is always water containing numerous substances in solution. Egg albumen is a colloidal mixture of proteins in water, containing also, however, various other substances suspended or dissolved in the water. A colloidal suspension of proteins varies in its consistency from that of a viscous liquid like egg albumen to that of so solid a substance as a firm gelatine. The differences in consistency depend in part upon the proportion of water present, and in part upon the size and arrangement of the protein particles.

An important characteristic of many proteins in the colloidal state is their tendency to undergo, under high temperatures and other conditions, the change known as *coagulation*. This change involves modifications in the physical state and probably in the chemical constitution of a protein. The albumen of a cooked egg is an excellent illustration of coagulated proteins. In many cases coagulation is irreversible; the coagulated protein can not again be brought into suspension in the medium from which it was separated.

Another significant characteristic of proteins and of other substances in the colloidal state is their general inability to pass through ordinary membranes, even through so permeable a membrane as a cell wall. Protein foods can not, therefore, pass from one cell to another unless the two cells are connected by openings of some size through the dividing walls. Such openings, it has been seen, are present in the walls between the cells of sieve tubes, and it is probable that sieve tubes serve for the translocation of protein foods.

94. Chemical Elements Utilized by Plants. In addition to the elements which enter into the composition of carbohydrates, fats, and proteins, namely, carbon, oxygen, hydrogen, nitrogen, sulphur, and phosphorus, at least four others are essential to the complete development of the more complex plants. These are calcium, magnesium, iron, and potassium. With the exception of

hydrogen, oxygen, and nitrogen, which are gases, all the elements named are solids. Nitrogen, iron, and sulphur may exist in the soil as elements; the others only in compounds. None of the elements of this list can be used by complex plants except in certain definite compounds. These elements may unite with one another and with other elements into such compounds as potassium sulphate, calcium phosphate, magnesium carbonate, and many others

FIG. 118. A series of cultures of plants; in culture 1 all the essential elements were present; in each of the other cultures at least 1 of these elements was absent. The cultures show the effects on growth of the omission of the respective elements; culture 2, lacking iron; 3, lacking magnesium; 4, lacking sulphur; 5, lacking calcium; 6, lacking nitrogen; 7, in distilled water only; 8, lacking phosphorus; 9, lacking potassium.

far more complex. Such compounds can be taken into a plant only in solution and only from soil or from water.

Although *nitrogen* constitutes nearly 80 per cent of the earth's atmosphere, it is not available in the elemental form as a nutrient material except to some simple plants and, through the agency of bacteria, to certain of the more complex ones. In general, it must be combined with oxygen and some other element in the form of a nitrate, such as potassium nitrate (KNO_3). Nitrates are absorbed by plants from the soil solution. A few familiar plants, such as rice, corn, and potato, can use nitrogen when combined with hydrogen in the form of ammonia (NH_3). Nitrogen forms a part of a very large number of substances occurring in plants. The type

of growth that characterizes any particular plant is often directly related to the amount of nitrogen available.

Phosphorus is a constituent of many highly complex organic substances in plant cells. It is essential to a rapid multiplication of cells, which is usually associated with active growth. Phosphorus is stored in large quantities in most seeds, and is taken from the soil in relatively large amounts during the early stages of growth of young plants.

Sulphur also is a constituent of some of the complex organic substances, in addition to proteins, needed for the maintenance of living matter.

Without *calcium* most green plants are unable to grow, and if calcium is not supplied to tissues already formed, the cells composing such tissues die and tend to disintegrate. This element also neutralizes acids, both within and without a plant, which otherwise might be injurious and might restrict or completely prevent the plant's growth.

Magnesium forms an essential part of the chlorophyll molecule. *Iron* is not a constituent part of this molecule, but when iron is lacking chlorophyll can not be formed. An insufficient supply of chlorophyll results in the diseased condition of plants known as "chlorosis." *Potassium* probably aids in the manufacture of carbohydrates and in their movement from cell to cell. Consequently, a diminution in the amount of either magnesium, iron, or potassium available to the plant would greatly decrease growth by limiting the formation of carbohydrates.

Other elements than those already mentioned, although absorbed in relatively small amounts, are as essential to the growth and development of green plants. *Boron, manganese,* and *copper* occur in very many plants, and these elements have been shown to exert a beneficial effect upon development. Others, including *aluminium, silicon, sodium,* and *zinc,* seem not to be essential; but their presence may be beneficial, and some of them have very specific effects upon the plants in which they occur. The presence of aluminium or zinc may cause definite variations in color and form in such plants as the hydrangea and pansy. The rôle of some of the elements mentioned may be stimulatory rather than nutritive.

CHAPTER X

THE UTILIZATION OF FOODS

95. Translocation. The chlorophyll-containing cells of stems or other organs are capable, like the green cells of leaves, of making certain sugars by photosynthesis. A similar statement applies to the cells of thousands of simpler green plants which possess no true leaves or stems, and many of which consist of but a single cell each. These carbohydrate foods may be used by the cells in which they are made, or they may be stored in the same cells, or in many-celled plants they may be moved to other cells. In all the larger plants, many cells more or less remote from those in which foods are made do not contain chloroplasts. Foods, in order to reach these distant cells, must pass in a dissolved condition, or possibly in some cases in an exceedingly finely divided state, out of the cells that made them and must be transported to their destination. Thus some glucose is used by the chlorophyll-containing cells that make it; but, being easily soluble, some of it is conducted to cells in other parts of the same plant.

If during photosynthesis the manufacture of sugars is more rapid than their use, sugars will accumulate in the cells in which they are formed. Commonly, however, under such conditions, much of the accumulated sugar is converted into starch, which appears in the form of grains in the chloroplasts (§ 91). Such an accumulation of starch occurs ordinarily during the daytime, but during the night the starch is usually changed back to a sugar which moves to and through the phloem to various regions of the plant; during this movement a portion of the sugar may pass out from the phloem at any level into other cells. The sieve tubes, by virtue of their great length and of the presence of numerous pores in their walls, appear to be especially suited for the rapid movement of foods. At certain times, and under certain conditions, foods may be transported in the elements of the xylem. All these movements of foods from place to place within the plant are included under *translocation*. Foods other than carbohydrates, such as proteins and fats, also are translocated from places where they are made to

places where they are to be stored, and from places of storage to regions where they are to be used.

96. Food-storage. Most of the foods whose manufacture has been discussed are often produced by a plant in far greater amounts than are immediately used. The surplus is stored. If photosynthesis is more rapid than the removal of its products, these products accumulate in the cells in which they originate and are ordinarily stored as starch in the chloroplasts; hence there may be a temporary storage in the chlorophyll-containing cells of leaves or of other organs. When starch is once formed, therefore, being a solid not readily soluble in water, it can not be moved. It must first be changed into a substance that is soluble, such as glucose or another sugar, if it is to be translocated. When sugar reaches a storage cell, some of it may be changed to starch, this change being effected by plastids, usually leucoplasts (§ 87).

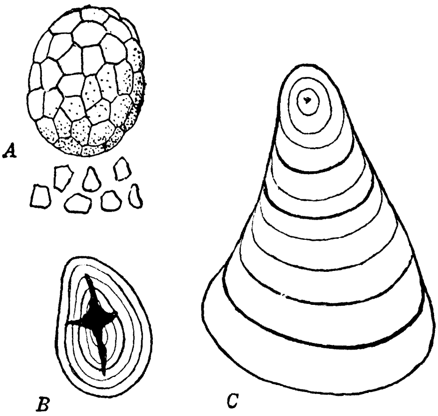


FIG. 119. Starch grains. *A*, compound and individual grains from the oat. *B*, grain from a seed of the bean. *C*, from the stem of canna.

The starch grains formed in leucoplasts are commonly larger than those formed in chloroplasts. Starch grains deposited in leucoplasts are stratified, being composed of successive layers deposited about an original small core. Their shapes vary greatly, those starch grains produced by each kind of plant having a more or less characteristic form (Figs. 111, 119). The layers that make up a grain are commonly of two different sorts. Some layers allow light to pass through rather freely and therefore appear clear in transmitted light. Layers of a second sort, alternating with those of the former type, do not allow light to pass through so readily; they appear, therefore, as comparatively dark, usually narrow zones. In many plants, including oats (Fig. 119, *A*) and rice, several starch grains are formed within each leucoplast; as these grains grow, they come into contact and commonly remain together as compound grains.

In occasional instances, comparatively large storage-starch grains are formed in chloroplasts instead of in leucoplasts. An example of this type of starch-formation is furnished by the relatively thick stems of *Pellionia*. The stems are green, since many of their cells contain chloroplasts. Photosynthesis may go on in these cells; and the accumulating sugars are transformed into starch. But the stems serve also as storage organs. Hence many of the starch grains, instead of being small temporary structures, as are most starch grains formed in chloroplasts, become large and similar in structure to the grains commonly deposited in leucoplasts (Fig. 120).

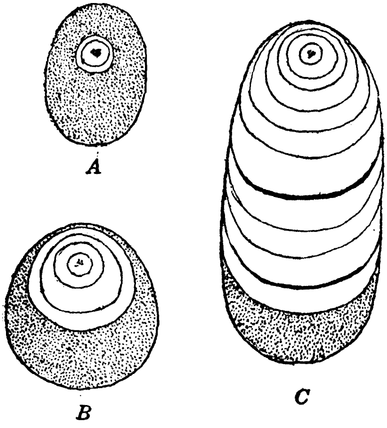


FIG. 120. Stages in the development of starch grains in chloroplasts of cortical cells of a stem of Pellionia. The chloroplast is shaded in each case. *A*, *B*, grains composed of but few layers. *C*, older grain with many layers.

Stored fats appear in various parts of cells as droplets of varying size. They occur in vacuoles and in the dense cytoplasm, as well as in, or attached to, chloroplasts, leucoplasts, and elaioplasts.

Protein foods also may be stored in the form of small globules (*aleurone grains*, Fig. 121). Aleurone grains are especially characteristic of the storage cells of the seeds of beans, peas, and other members of the same family, as well as of a particular layer of the kernels of the cereal grains. In the castor bean, the aleurone grains are comparatively large and of complex structure.

The portions of different plants in which foods are stored vary greatly, depending largely upon the length of life of the plant. In annual plants foods are stored chiefly in seeds and fruits. The corn kernel is a fruit in which are stored quantities of starch and fats and some proteins; the bean seed is rich in carbohydrates and proteins. In trees and shrubs, as well as in other perennials, storage may occur in any of the living tissues of the vegetative organs, most frequently in those of stems and roots. A potato tuber is an enlarged underground branch, or part of a branch, many of whose

cells are packed with starch; a head of cabbage consists chiefly of leaves containing much water as well as some fats, carbohydrates, and proteins. The sugar beet has a much-enlarged root in the sap of whose cells large quantities of cane sugar are dissolved.

97. Digestion; Enzymes. The term *digestion* is applied to those chemical changes in a substance which render that substance soluble and capable of diffusing readily through cell membranes. Many stored foods, such as starch, are insoluble or practically so in cell sap, and hence must be digested before they can be utilized

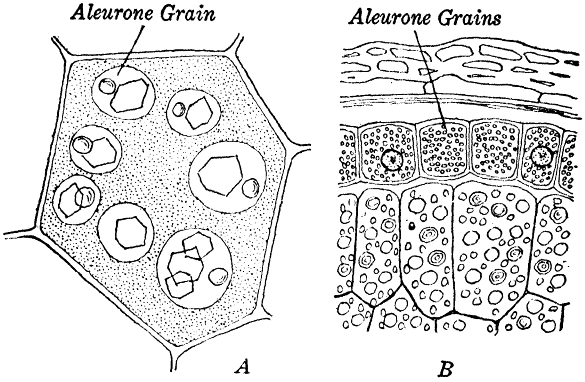


FIG. 121. Aleurone grains. *A*, cell of the castor bean containing large, complex grains. *B*, cross section of the outer portion of a kernel of corn, showing the layer of cells which contain many small aleurone grains. After Strasburger.

or translocated. Some other stored foods, such as cane sugar, while soluble in cell sap, do not diffuse readily through cell membranes; they also, therefore, must be digested before being translocated. The protoplasm of plant and animal cells produces special substances known as *enzymes* whose function it is to bring about or to accelerate chemical changes. Each class of compounds, such as fats, proteins, or starch, is in general acted upon by a particular type of digestive enzyme. Starch is digested by *diastases,* fats are digested by *lipases,* proteins by *proteases,* and cane sugar is changed into two simpler sugars (dextrose and levulose) by *invertase.* In the course of any such process the enzyme concerned is not used up, and exceedingly small quantities of a digestive enzyme are capable, consequently, of digesting large amounts of the particular food upon which it acts. Some foods are digested quite as well outside

a living cell as in it, when they are brought into contact under appropriate conditions with the proper enzyme. An extract of diastase, for example, derived from barley kernels, will digest starch if placed with the starch in a little water in a test tube. Experiments such as this demonstrate that enzymes are distinct from living matter, since they can be extracted from cells without loss of their characteristic properties by processes that remove or kill the living matter.

Although enzymes play a conspicuous and important part in digestive changes, it must not be thought that these are the only processes with which enzymes are concerned. As a matter of fact, they take part in most if not all of the chemical changes, including those involved in the manufacture of foods and other compounds, that go on in living cells. The several steps in photosynthesis itself may possibly be due to specific enzymes. When living matter brings about chemical changes, therefore, it does so largely through the agency of enzymes that it has produced. It follows that a great variety of enzymes are present in every living cell.

98. Living Matter. In all the living parts of a plant, substances are continually being changed from one form to another. In some cases, simpler compounds are changed to more complex ones; in others, the change is from a more complex to a simpler form. The actual incorporation of non-living substances into the living matter itself is *assimilation*. Assimilation usually involves digestive action; and it always involves numerous building-up processes in which enzymes are often concerned. One of the characteristics of living matter is its power of growth and repair—that is, its ability to manufacture new matter like itself out of foods. Another characteristic is its instability—the readiness with which it undergoes changes as a result of changes in the conditions which surround it. At all times, living matter is being continuously built up and continuously broken down. It possesses also the capacity of liberating and of utilizing for various purposes energy stored in foods.

Living matter is probably not a single substance, but rather a combination of substances more or less closely united physically and chemically, and definitely arranged and organized in each particular kind of cell. As yet, all attempts to determine the exact chemical composition of living matter have failed, because in any such attempt its condition is so markedly changed that it ceases to be living. At best, therefore, an analysis can furnish only

an indication of the substances which entered into the living matter.

By an examination of living cells it is possible to determine something of the physical relations of the substances present. A large part of living matter is always water in which various substances are dissolved. The less liquid portions of living matter include carbohydrates, proteins, and fats in a colloidal state. The particles are often aggregated to form granules, globules, and strands of various forms and sizes which are large enough to be visible under a microscope. These larger aggregations are themselves suspended in the more transparent, and often more liquid, portion of the living matter. Very often this liquid portion contains ultramicroscopic droplets which may be aggregated into visible drops or vacuoles that are more transparent than the remaining liquid. It is evident that there is a still finer structure inherent in living matter which microscopes of the highest powers can not reveal, and upon which as yet only indirect and conflicting evidence is available.

99. Growth. Growth is commonly thought of as an increase in size. Frequently increase in size—that is, in volume—involves an increase in the amount of water present in the plant, as well as an increase in the amount of those substances other than water which remain if the plant is completely dried. In many instances, however, plants or some of their organs increase greatly in their content of substances other than water, such as starch, sugars, and the like, although such plants or organs do not increase appreciably in volume. Such an increase in materials other than water is often referred to as growth, whether or not it is accompanied by an increase in size. On the other hand, many plants, especially those containing large amounts of stored foods, when placed under conditions favoring development, may increase greatly in size, largely through the absorption of water, but may actually decrease in the amount of substances which remain when the plants are dried. Such an increase in size is also often considered as growth even though there is no increase in the amount of any substance present other than water. Thus growth, depending upon the sense in which the word is used, may be measured either by increase in volume, by increase in dry weight, or in both ways.

Growth of a plant and of its various organs, in any sense of the term, depends upon the division and growth of the individual cells of which it is composed. Because the greater portion of the

plant consists of mature cells, not all its cells at any one time are concerned in growth. As has been seen, the cells in the embryonic regions of roots and stems are both growing and dividing; growth here consisting mainly in an increase in the amount of living matter. In regions of elongation the enlargement of cells is brought about almost entirely by an increase in their water content. In regions of maturation growth involves an increase in the amount of cell wall material. Cells produced by cambial activity undergo a similar sequence of phases of growth: increase in living matter, increase in water content, and the deposition of cell wall material.

The amount and kind of growth that a plant undergoes depend not only upon the total quantities of foods present or being manufactured, but also upon the *proportional* amounts of water as well as of mineral nutrients available. A plant may possess an abundance of carbohydrates, but in the absence of sufficient water they are not utilized; or, if it has both carbohydrates and water, and lacks certain elements which these do not contain, the carbohydrates and water are not combined into other substances.

When a biennial or perennial plant resumes growth in the spring, its growth at first depends upon the utilization of reserve foods, together with the absorption of water and of mineral nutrients. Plants which lost their leaves in the autumn must produce new leaves in the spring, at the expense of stored foods, before photosynthesis can be resumed. If the surviving part of the plant is an underground portion only, such as the tuber of a potato, growth goes on at the expense of the stored foods until a leaf-bearing shoot has been formed. In the leaves of evergreen plants, such as a pine, the green substance present in the leaves in the spring is not true chlorophyll, at least in regions with cold winters. With the advent of higher temperatures in the spring, however, the re-formation of chlorophyll in such leaves quickly makes possible the resumption of carbohydrate-manufacture.

The development of the embryonic plant in a germinating seed to the point at which it can carry on photosynthesis involves the use of foods stored either in the seed leaves of the embryo or in tissues of the seed outside the embryo. The extent to which the reserve foods in a seed are used in the early development of a young plant may be determined experimentally by removing all or most of these foods. For example, in a bean embryo the two seed leaves

contain nearly all the reserve foods. Their utilization may be shown by comparing the amount of growth of two young bean seedlings of similar age; both seed leaves are removed from one seedling and both are left attached to the second. During several days following, the plant with both seed leaves will develop the more rapidly and the one from which both seed leaves have been removed will develop more slowly, if it continues to develop at all. There is thus a direct proportional relation between the growth of the young seedling and the amount of foods available for its development. The later the seed leaves are removed during the period of germination and early growth of the seedling, the less pronounced is the effect of such removal upon the young plant. In fact, the seed leaves are shed by the bean plant itself after most of the foods which they contained have been utilized.

Plants without chlorophyll must acquire foods directly from living green plants, or must utilize foods which were originally manufactured by such plants. Even in green plants, especially in the more complex ones, there are many organs and living cells that lack chlorophyll. The foods required by such cells for maintenance of their living matter, growth, and reproduction must be conducted to them from other cells which have made more foods than were needed for their own use.

100. Secretion. The production by plant cells of compounds which are stored for short or long periods is *secretion.* Such foods as sugars, starch, fats, and proteins are secreted. The formation of chlorophyll and other pigments and the deposition of cellulose and other substances in the form of cell walls are processes of secretion. In addition to those already mentioned, a vast number of substances are secreted by the cells of various plants. These substances include glucosides and alkaloids, many of which are of medicinal value; volatile oils, which cause the characteristic odors of plants; organic acids, such as malic acid found in apples, and citric acid in lemons, oranges, and grape fruits; mucilages, oleoresins, latex (milky juices), and tannin. Many secreted substances are reserve foods; others are useful in a variety of ways to the plant which makes them; but some are by-products or waste substances. The deposition or extrusion of useless or possibly harmful substances is often referred to as *excretion;* but it is not easy to distinguish sharply between excretion and secretion.

101. Pigments. Certain secreted pigments, especially the chlorophylls, carotin, and xanthophyll, which are present in plastids, have already been described. Certain other pigments that are secreted by plant cells occur, not in plastids, but in solution in the cell sap. Most abundant of these water-soluble pigments are the *anthocyans*, which are usually red or blue. In some plants anthocyans are present in varying amounts at all times. In others they appear only in the spring or in the autumn. They are abundant in the roots of the red beet and the radish, in red onion bulbs, in the leaves of some plants, such as Coleus, and in many red and blue flowers and fruits. In some plant parts, these pigments appear only in cells of the epidermis; in others, they occur in cells of various tissues.

The formation of an anthocyan is dependent especially upon the presence of large amounts of sugars. When conditions are such that sugars are being used rapidly by a plant so that they do not accumulate, anthocyans are not formed. At low temperatures sugars accumulate and anthocyan-formation results. Many plant parts are brilliantly red in early spring and in autumn, because of the abundance of sugars and the consequent formation of anthocyans.

Although the functions of anthocyans have not been definitely determined, it is possible that they aid in the absorption of certain rays of light which would be injurious to chlorophyll. Anthocyans absorb some light energy, which is converted into heat, so that under like conditions red leaves have a higher temperature than green ones. Such rise in temperature may accelerate the activities of living matter, and perhaps aids in protecting a plant from the effects of low temperatures in the surrounding air.

The brilliant colors characteristic of autumn leaves in temperate regions result from the presence of pigments. The yellow colors are due to the yellow pigments present in chloroplasts. During the summer chlorophyll is usually formed about as rapidly as it is destroyed, but as autumn progresses the production of chlorophyll is slower than its destruction, so that the green color fades, leaving only the color of the yellow pigments. Both low temperatures and drought tend to check the formation of chlorophyll, but frost is not necessary to its disappearance. It is a matter of common observation that leaves often become yellow during dry periods even in summer. Bright red colors are due to anthocyans

which are produced in many plants in the autumn. Autumnal conditions favor the accumulation of sugars in leaves and hence the formation of anthocyans. When a leaf is alive, the cell walls are light-colored and translucent. They become brownish upon the death of the cells. The protoplasts often blacken after death. In these ways the brown and black colors of autumn leaves are caused. Various combinations of yellow, red, brown, and black colors produce intermediate shades or cause a mottling of the leaves.

102. Respiration. It has been seen that in photosynthesis a part of the energy which comes to the earth's surface as light is used in the production of a sugar out of carbon dioxide and water. In other words, some of this energy has entered into, and is bound up in, the sugar itself. If by any means the sugar is decomposed into simpler substances, energy is set free. It would be possible completely to release the bound-up energy by changing the sugar back to carbon dioxide and water.

Since all foods utilized by animals come directly or indirectly from plant cells, the continued existence of animals as well as of plants depends upon the available energy accumulated in the process of photosynthesis. Man makes use of such stored energy not only for his bodily needs but also in various other ways. The use of fuels as a source of heat or of mechanical energy is, in the last analysis, merely the transformation of energy previously absorbed from the sunlight by chlorophyll. The use of wood as a fuel involves the utilization of energy that has thus been accumulated comparatively recently, whereas coal and petroleum represent stores of energy accumulated millions of years ago.

A living plant requires a source of energy for carrying on its various functions, such as the formation of the more complex foods, assimilation, growth, and movement. Since for most of these functions the energy of light can not be used, as it is in photosynthesis, some of the foods already built must be destroyed in order that their stored or potential energy may be liberated. In plant cells carbohydrates and other organic substances, when they are utilized as foods, are to a large extent decomposed by processes analogous to, but essentially different from, combustion, and the energy so released is utilized by the cells in which the decomposition occurs. The process by which, in living cells, energy is obtained or released through the destruction of foods is

respiration. In respiration the foods destroyed are not merely the sugar or sugars first formed in photosynthesis; they may include a considerable variety of substances, among them fats and proteins, which like sugars possess stored-up energy. Commonly, though not in all cases, respiration entails the absorption of free oxygen and its combination with the substances undergoing destruction, which thus become oxidized. Land plants obtain oxygen needed for respiration from the air, including that present in the interstices of the soil. Plants living submerged in water are dependent upon oxygen that is dissolved in the water. It has been seen that cells carrying on photosynthesis liberate oxygen, which is available for their respiration as well as for that of other cells.

If the substance being respired is a carbohydrate, and if it is completely oxidized, carbon dioxide and water are produced. Hence the respiration of carbohydrates is in some of its effects the reverse of photosynthesis. It will be remembered that in photosynthesis carbon dioxide and water are combined, oxygen is liberated, sugar is formed, and energy is stored. During respiration of a sugar, oxygen is combined with the sugar, carbon dioxide and water are re-formed, and the stored energy is released. Oxygen is set free as a result of photosynthesis; carbon dioxide is set free as a result of respiration. Unlike photosynthesis, however, respiration is going on all the time, night and day, in every living cell, whereas photosynthesis takes place only in chlorophyll-containing cells and only in the presence of light. It is, therefore, only when the rate of photosynthesis exceeds the rate of respiration that oxygen is given off by a leaf, and, conversely, only when respiration is more rapid than photosynthesis is carbon dioxide given off. If the two processes were to go on at exactly equal rates, neither carbon dioxide nor oxygen would be evolved from the cells concerned. Likewise, since the initial sugar is made only through photosynthesis, and since foods are constantly being destroyed through respiration, it is only when the quantity of materials built up exceeds the quantity destroyed that a green plant can actually gain in dry weight. A green plant grown in the dark loses in dry weight because its stored foods are respired; a similar plant grown in the light gains in dry weight because photosynthesis is possible and because, although respiration is going on, more foods are manufactured by the plant in the light than are destroyed.

A part of the energy released in respiration appears in the form of heat; but because of the slowness of the process, and because of the large radiating surface of the plant compared with the amount of heat being radiated, it is difficult to measure the heat generated at any specific point. When respiration is very active, however, as in some germinating seeds, the liberated heat can be measured. Provided special precautions are taken, a rise in temperature may often be demonstrated. During the active growth of bacteria in certain media, temperatures of 35° to 40° C. are not uncommon, as compared with ordinary room temperatures of 18° to 20° C.

That large quantities of carbon dioxide are given off in respiration can be determined by passing air freed from carbon dioxide through a vessel containing germinating seeds (Fig. 122),

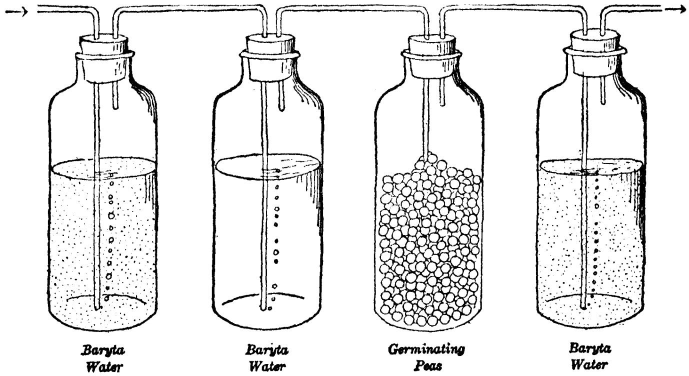


FIG. 122. An experiment demonstrating the evolution of carbon dioxide during respiration. The baryta water in the first bottle removes all carbon dioxide from the air, as shown by the lack of a precipitate in the second bottle; the air then passes into the third bottle, containing germinating peas; the air passing from this into the last bottle again contains carbon dioxide, and a precipitate is formed.

and then testing the air with baryta water for the presence of carbon dioxide—a white precipitate being formed when carbon dioxide is passed into baryta water.

When green leaves are used to illustrate the liberation of carbon dioxide in respiration, it is necessary to place them in darkness, since in light the carbon dioxide produced by respiration might be utilized in photosynthesis and therefore not liberated from the leaves. If, then, green leaves are placed in a flask containing air, and the flask is closed and kept for a time in darkness, it is possible

to determine that carbon dioxide has been liberated by testing the gases in the flask with baryta water and noting the precipitate formed. That most of the oxygen originally present in the air contained in the flask has been consumed by these leaves can be shown by the effects produced upon a lighted splinter lowered into the flask containing the leaves, as compared with the effects produced upon a splinter lowered into a flask containing air alone. The splinter in the flask containing air will continue to burn until most of the oxygen has been consumed, whereas that in the flask containing the leaves is immediately extinguished.

103. Anaërobic Respiration. Another type of respiration differs from that just discussed in the fact that, while foods are destroyed and energy is released, no atmospheric oxygen is absorbed during the process. Instead, the elements in the molecules of which the foods are composed are rearranged into other substances, and the oxygen necessary for respiration is released. Since these changes take place in the absence of atmospheric oxygen, the process is called *anaërobic respiration* in contrast to *aërobic respiration.* Anaërobic like aërobic respiration is a means by which the respiring organism releases energy. Anaërobic respiration may be illustrated by inserting several pea seeds previously soaked in water into the mouth of a test tube filled with mercury and inverted over a dish of mercury. The seeds will rise to the top of the mercury in the test tube. After a time, as the seeds respire, the mercury will be forced down and out of the test tube by the pressure of the carbon dioxide produced. Since in this type of respiration the foods may not all be completely broken down into carbon dioxide and water, more foods may be consumed in proportion to the amount of energy released than in aërobic respiration, and substances are often formed which are poisonous to the plant. At times very high temperatures are generated in the course of anaërobic respiration.

In higher plants respiration of this type is but a temporary substitute for aërobic respiration, and such plants will eventually perish if permanently deprived of atmospheric oxygen. Many bacteria, yeasts, and molds, however, may use only small amounts of atmospheric oxygen. For such organisms anaërobic respiration is therefore the fundamental process concerned in the release of energy. Anaërobic respiration on the part of these simple organisms is *fermentation.*

104. Metabolism. The whole complex of material and energy changes which go on within the plant is *metabolism.* Metabolism includes constructive processes, such as photosynthesis, other forms of food-manufacture, and assimilation, as well as destructive processes, most conspicuous among which is respiration. An excess of constructive over destructive metabolism results in an increase in the amount of those substances which would remain if the plant were dried. An excess of destructive over constructive metabolism results in a decrease in the amount of such substances present. It is only an excess of constructive over destructive processes that permits of the continued existence and growth of a plant body as a living unit. Every living animal, and every living plant except some of the bacteria, is ultimately dependent upon photosynthesis for its existence, because at present this is the only efficient means of combining inorganic substances into a food—that is, into a store of reserve energy.

CHAPTER XI

STIMULUS AND RESPONSE

105. Irritability. As has been seen (§ 10), the dense cytoplasm in a cell of a leaf of Elodea may be in motion at ordinary room temperature. If the temperature is gradually raised, movement becomes more and more rapid, until at a particular point (about 37° C.) the greatest rapidity is reached. As the temperature is raised further, movement becomes slower, and at about 38.7° C. it ceases entirely. If, on the other hand, a cell showing streaming at room temperature is cooled, the motion becomes gradually slower until at about 0° C. it stops. It is evident that this form of activity of living matter is influenced by an external condition, namely, temperature. All other forms of activity of living matter are likewise affected by this and by other external conditions. Any external condition that affects a process going on within a cell is a *stimulus*. The external condition, in order to serve as a stimulus, must exert some force upon the living matter; a stimulus, therefore, implies an expenditure of energy. The change within the cell which results from the application of a stimulus is a *response*. In the case of streaming cytoplasm, the response is a quickening or slowing of the rate of movement. In very many instances the response to a stimulus is similarly a slowing or an acceleration in the rate of some intracellular process. Responses, however, include changes of any nature in the activities of a cell, including the initiation of a new process, or changes in activities common to a group of cells such as a tissue or an organ. A response involves an expenditure of energy on the part of the living matter. But the energy which is expended in the response has no necessary relation to the energy that was manifested in the stimulus. The energy of the response is energy that was already present, but in latent form, in the living matter; not that which was supplied by the stimulus. A stimulus is recognizable as a stimulus only if it produces a perceptible response. Practically, therefore, only those stimuli are treated as such which result in a response that can in some way be observed.

The capacity to respond to a stimulus is *irritability*. Irritability may be manifested by non-living as well as by living matter, but living matter is marked by the ability to respond readily in a variety of ways to a great variety of stimuli. Irritability is considered, therefore, one of the fundamental characteristics of living matter.

As just noted, streaming movements cease if the cells of an Elodea leaf are cooled to about 0° C., or if they are heated to about 38.7° C. These temperatures are respectively the *minimum* and the *maximum* temperatures for streaming. The movement is most rapid at about 37° C., which is the *optimum* temperature for streaming. In general, an external condition, such as temperature, in its effect upon a particular activity has a minimum, an optimum, and a maximum point. Among the stimuli that affect cytoplasmic streaming in the cells of an Elodea leaf are, besides temperature: mechanical shock, electric currents, illumination, and the proportions of salts, acids, alkalis, sugars, oxygen, or carbon dioxide in the liquid surrounding the leaf.

106. Other Relations of Temperature to Living Matter. If the rise in temperature is stopped as soon as streaming ceases, and the leaf is slowly cooled, streaming may begin again. A stoppage of the streaming movement, therefore, does not necessarily mean that the protoplasm is dead. Death involves the cessation of a complex of activities which characterize matter in a living condition. Each activity of living matter has its minimum, optimum, and maximum temperatures, and these temperatures may be different for each of the various activities of a single cell; or they may be different for the same activity in cells of different kinds. In general, the temperature range for activities characteristic of living matter is between 0° and 50° C. Under some conditions, however, especially when the protoplasm contains relatively little water, such temperature limits may be greatly exceeded without a resultant death of the cells concerned. Seeds of low water content may be kept alive for long periods at temperatures of from 90° to 100° C. without causing the death of their cells. Many bacteria are killed at 70° C., but some will endure temperatures above 90° C. Certain bacteria in a resting condition can be killed only by prolonged heating at 100° C. At the other temperature extreme, some seeds and some dormant bacteria can endure the temperature of liquid hydrogen (252 centigrade degrees below the freezing point).

The temperature of the air, as well as that of the soil or water with which a plant is in contact, affects the activities of the plant's component cells, and therefore the activities, including growth, of the plant as a whole. Any kind of plant thrives best within a certain range of temperature which is much narrower than that within which the plant can remain alive. The more the temperature varies from this favorable range the less vigorously does the plant grow. Hence, the distribution of plants on the earth's surface is in part determined by temperature.

Plants do not ordinarily possess the relatively high internal temperatures which characterize the bodies of many of the larger animals. Instead, the internal temperatures of most plants are not greatly different from the temperature of their environment. In this connection it is of interest to note the effects of transpiration on the temperature of leaves. Rapid transpiration has a marked cooling effect, and on a hot summer's day may result in lowering the temperature of a leaf several degrees below that of the surrounding air. On the other hand, vigorously growing regions of plants may develop an internal temperature several degrees higher than that of the environment. In such cases respiration goes on very rapidly and much of the released energy takes the form of heat. These facts explain how such plants as the skunk cabbage may be seen growing through snow and frozen soil in early spring.

107. Responses to the Stimulus of Gravity. All processes going on in living organisms are affected by many environmental factors. Of these factors gravity is the only one which acts constantly in the same direction and with the same intensity at any point on the earth's surface. Gravity affects the direction of growth of plants. In general, stems grow vertically upward, primary roots vertically downward, and branches, leaves, and branch roots grow transversely or at widely varying angles to the direction of the force of gravity. The ability of plants or of their parts to respond in these various ways to gravity as a stimulus is *geotropism*. Organs which respond to the stimulus of gravity by growing toward the center of the earth are *positively geotropic;* those which respond by growing away from the center of the earth are *negatively geotropic;* those which grow at right angles or obliquely to the direction of the force of gravity are *transversely geotropic*. To illustrate responses to gravity, seedlings of bean or corn whose roots and stems are a few centimeters long may be placed in a moist chamber

with the stems and roots at various angles to the direction of gravity. In a few hours the stems will have turned upward and the primary roots downward.

In most roots growing in the soil, the part that is capable of receiving the stimulus of gravity, and which is therefore said to *perceive* the stimulus, appears to be the terminal portion, including

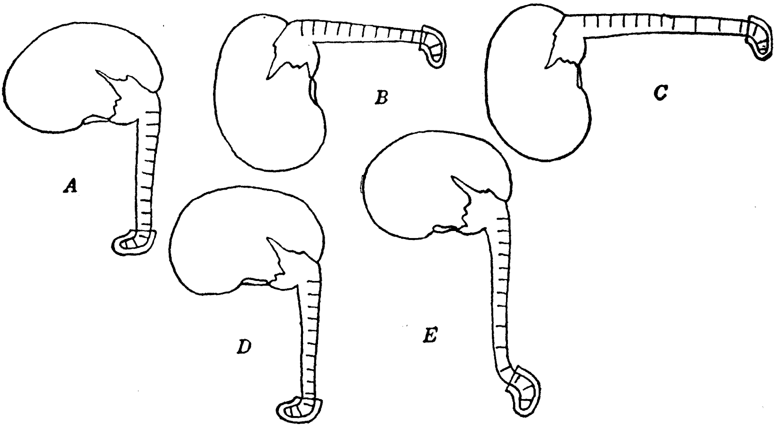
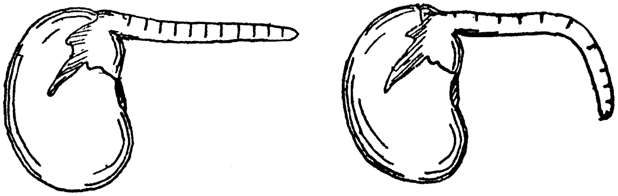


FIG. 123. Roots with tips in glass slippers. *A* shows tip bent at right angles. *B*, same root placed with its tip vertical. *C*, same root after 18 to 20 hours. *E*, curvature 18 to 20 hours after the root is placed in position *D*.

the root cap; the responding portion is farther back, in the region of elongation. The location of the perceptive portion may be shown by making root tips grow into small glass slippers (Fig. 123, *A*) so that the terminal few millimeters of each root are bent at right angles. One of these roots is then placed horizontally with its bent tip turned downward (Fig. 123, *B*). Since the perceptive portion of the root is now in a vertical position, no effect is transmitted to the horizontally placed region of elongation; consequently no further change in form occurs, and the region of elongation continues to extend in the direction in which it is placed (Fig. 123, *C*). If, however, the root is so placed that the region of elongation is vertical and the bent tip horizontal (Fig. 123, *D*), the root will curve until the perceptive portion is in a vertical position (Fig. 123, *E*).

The location of the responding portion can be determined by marking with India ink the primary root of a bean seedling at intervals of one millimeter and placing the seedling in a moist

chamber with its root in a horizontal position (Fig. 124). After 24 hours it can be determined by measuring the distances between



A B

FIG. 124. *A*, bean seedling whose root has been marked at equal intervals and placed in a horizontal position. *B*, the same seedling 24 hours later.

markings that the region of downward curvature corresponds with that of greatest elongation. This curvature observable in the region of elongation is due to an elongation at different rates on opposite sides of the root. The experiments just described, taken together, show that in this root the region of perception and the region of response are distinct.

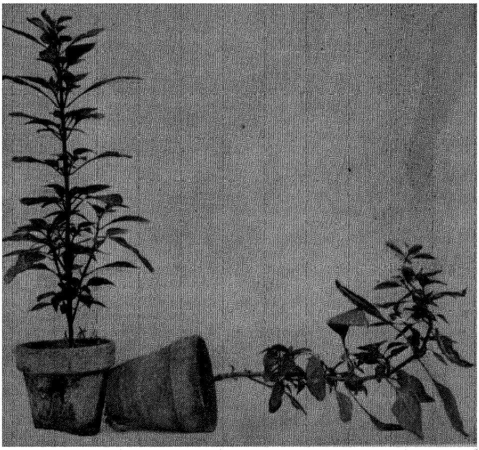


FIG. 125. At the left, a plant of Iresine in the ordinary position; at the right, a plant which has been turned on its side. The negative response to the stimulus of gravity consists in bending at the nodes as well as in the elongating region near the tip.

In the majority of stems both the perception of the stimulus of gravity and the response to this stimulus are localized in the region of elongation. The location of the responding portion of a stem may be shown by marking with India ink sunflower or tomato stems at equal intervals and placing the plants parallel to the earth's surface. After a few hours it will be found that an upward curvature has occurred in the elongating internodes; the mature internodes show no response. However, in some stems geotropic response is not localized exclusively in the region of elongation.

If the relatively mature stem of Iresine (Fig. 125) is placed in a horizontal position, upward bending will occur at each of the younger nodes, as well as in the region near the tip where the internodes are elongating. If a similar experiment is performed with the stem of some grass, such as wheat, bending will occur only at the nodes. This is because of the delayed maturation of the nodal tissues (§ 34).

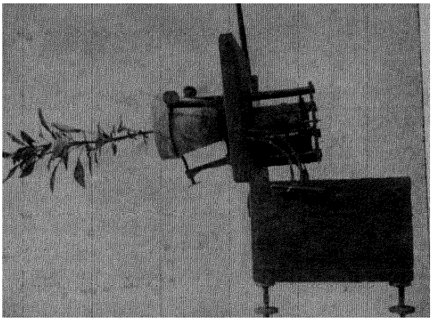


FIG. 126. An apparatus (clinostat) for rotating plants slowly about a horizontal axis, constantly changing their relation to the direction of the stimulus of gravity.

To determine whether such changes in position of stem and root are geotropic responses, it is necessary to counteract the action of gravity as a stimulus and to observe the direction of growth under the new conditions. This can be done by rotating the plant slowly about a horizontal axis, thus constantly altering the plant's relation to gravity (Fig. 126). Gravity is now no longer operating as a one-sided stimulus. Under such conditions the stem does not grow vertically upward nor the primary root vertically downward, but

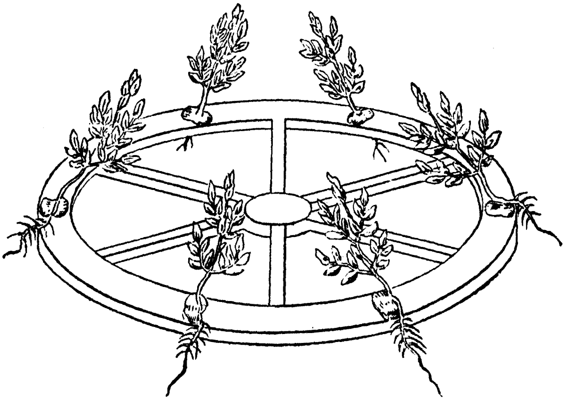


FIG. 127. Knight's experiment, in which the stimuli of both centrifugal force and gravity are acting upon stems and roots.

these organs tend to grow horizontally—that is, in the directions in which they were placed when the experiment began.

In another experiment, first performed by Knight in 1805, the seedlings are placed on the rim of a horizontally revolving wheel (Fig. 127) and the wheel is rapidly rotated. The primary roots of the seedlings now grow diagonally downward and outward, while the stems grow upward and inward. The stems and roots are responding both to the stimulus of gravity and to that of centrifugal force.

It is impossible as yet to explain fully how the stimulus of gravity is perceived and how it is transmitted from the perceptive to the responsive portions of a root or stem. Experimental evidence seems to indicate that geotropic curvature is influenced mainly by the production of growth-regulating substances and by their unequal distribution under the influence of gravity. The difference between the reactions of roots and those of stems to the stimulus of gravity is explained by a difference in the action of the growth-regulating substances in these respective organs. It is thought that, in a root which responds positively, a growth-regulating substance is produced in the tip. If the root is placed horizontally, the accumulation of this substance on the lower side of the root results in a slowing of growth on that side. The upper side of the root continues to grow, and the consequence is a downward bending of the root in the region of elongation. If a negatively geotropic stem is horizontally placed, an accumulation of a growth-regulating substance in the lower side *accelerates* growth on that side, and the stem bends upward. In the two cases just cited the growth-regulating substance is the same; but the responses that it causes in root and stem are opposite in kind.

Not all investigators accept the explanation of geotropic response just outlined, and other explanations of such response have been proposed.

108. Responses to the Stimulus of Light. Unlike gravity, light is neither constant nor uniform in amount, direction, or intensity. Like gravity, light affects the direction of growth of plants. Stems are usually *positively phototropic*, bending toward a source of light. Branches and leaves are usually *transversely phototropic.* Some roots, such as those of certain members of the mustard family, are *negatively phototropic.*

Not all organs of plants are sensitive to light as a stimulus.

Phototropic responses are in general characteristic only of the aërial parts of plants, although the sensitivity to light is in no way connected with the presence of chlorophyll. Such underground organs as roots and rhizomes, which grow in darkness, usually show no reaction to light.

To determine the regions at which phototropic responses occur, the stems of young plants, as of sunflower or geranium, are marked with India ink at intervals of 5 mm. (Fig. 128) and then grown in darkness for 24 hours. The intervals are then remeasured.

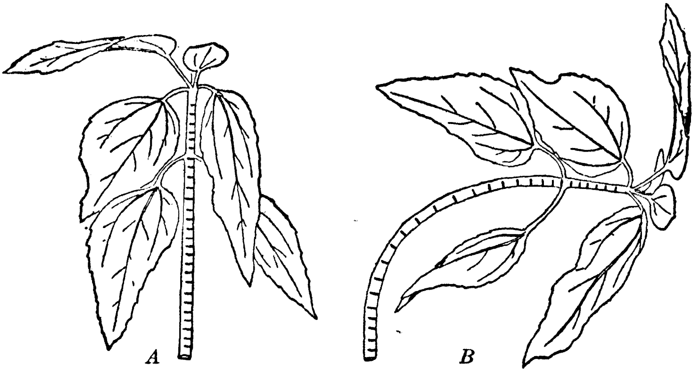


FIG. 128. *A*, part of a sunflower plant with its stem marked at equal intervals. *B*, the same plant after exposure to a one-sided illumination. The bending occurs in the region of elongation.

The plants are next so placed that they are illuminated from one side. In a few hours the stems will show phototropic curvature, and it can be determined by measuring the intervals between the marks that the regions of curvature correspond with the regions where the greatest elongation has occurred. Not all parts of any particular organ are equally sensitive to the stimulus of light. In general, the apical part of a stem is most sensitive; the older portions also are sensitive but usually to a lesser degree, the sensitiveness decreasing as the distance from the tip increases.

The positions of some leaves are changed in response to light stimuli by alterations in the direction of growth of their petioles. The new position may be either temporary or permanent. The leaves of house plants such as the geranium which are growing in a window change their positions so that the upper surface of each blade faces the source of light. That it is the blade rather than the petiole which perceives the light stimulus can be shown

by wrapping the petiole of a young leaf of nasturtium or of begonia with tin-foil so as to exclude all light, and by covering in the same way the blade of a similar leaf whose petiole is left exposed. If the leaves so treated are now illuminated from one side, only the leaf with the exposed blade will respond by a curvature of its petiole.

The response of most broad foliage leaves to light as a stimulus may occur, not only in the petioles, but also in the growing parts of the blades or in parts still capable of growth. In general, each such leaf finally assumes a relatively fixed position, which tends to be such as to expose the surface of the blade most directly to the incident rays of light. The movements of leaves in attaining their fixed positions may be due to curvature, increase in length, and torsion of the petiole, of the leaf blades, or of both. The blades often thus become so arranged that they do not greatly overlap or shade one another. Leaf mosaics (§ 60) are produced in this way.

In previous paragraphs it has been noted that light affects the *direction* of growth. That it also affects the *rate* of growth and the form of the plant becomes evident when bean or potato plants grown in darkness are compared with those grown in light (Fig. 110). The plants grown in darkness have very long, slender stems because of the greatly elongated internodes; their leaves are small, have long petioles, and show little differentiation in the internal structure of the blades; and because chlorophyll is not developed the plants have a pale yellowish appearance. The differences in these cases illustrate the general fact that the type of growth of plants is profoundly affected by the intensity of illumination. The precise effect of light stimuli varies greatly, however, between plants of different species and even between different organs of the same plant. For example, stems and branches are not always more elongated in weaker illumination; on the contrary, the branches on the shaded side of a tree are often shorter than those that are directly exposed to light. The effects of intense illumination upon the growth of plants adapted to shady conditions are very different from its effects upon plants which ordinarily grow in sunny localities.

Experiments suggest that the tips of phototropically responding organs form growth-regulating substances which are redistributed under the influence of light, and that these substances cause

a retardation of growth on the lighted side and a more rapid growth on the shaded side, the result being a curvature of the responding organ.

109. "Long-day" and "Short-day" Plants. Both the intensity of the light to which a plant is exposed, and the length of time during which it is illuminated, materially affect its development. If a green plant is grown under conditions which are favorable except that illumination is feeble, the character of growth will be altered and the production of flowers will be delayed and may not occur at all. When such a plant is placed in light of greater intensity it produces flowers.

If, on the other hand, the intensity of illumination is kept favorable, the length of daily exposure to light affects the amount and type of growth. Some plants flower and fruit much earlier when the period of exposure to light is less than 12 hours in each 24. Among such "short-day" plants are ragweed and some varieties of soybean. Other plants flower and fruit earlier when the daily exposure to light is more than 12 hours. "Long-day" plants in this category include the tomato, radish, and lettuce and some biennials such as sweet clover. Still other plants, one of which is buckwheat, show little or no response in this respect to changes in the length of daily illumination.

110. Responses to the Presence of Water. The direction of growth of young roots is often affected by the presence of a local supply of water in the soil. In such a case the distribution of water from the local source results in the presence of varied proportions of water in different parts of the soil, and the roots may grow toward the region in which water is most abundant. The effect of a stimulus of this nature on the direction of growth of roots may be shown by filling a large box with dry soil and imbedding in the soil near one end of the box a porous cup filled with water. The water will percolate into the soil, so that the soil near the cup is moister than that farther away (Fig. 129). If bean seeds germinate in the soil at some distance from the cup, their roots, when formed, will grow toward the cup until they reach a region in the soil containing a certain proportion of water. Here the primary root no longer responds to the stimulus supplied by the presence of water but, reacting to the stimulus of gravity, grows downward. The secondary roots usually continue their horizontal growth. It is evident from this experiment that

both water and gravity play a part in determining the direction of growth of roots in soil. The stimulus supplied by the presence of water is, however, often the stronger of the two, as is illustrated by the growth of roots along ditches, tile drains, and irrigation canals.

That the proportion and distribution of water in the soil may have a formative influence is shown by the roots of many desert

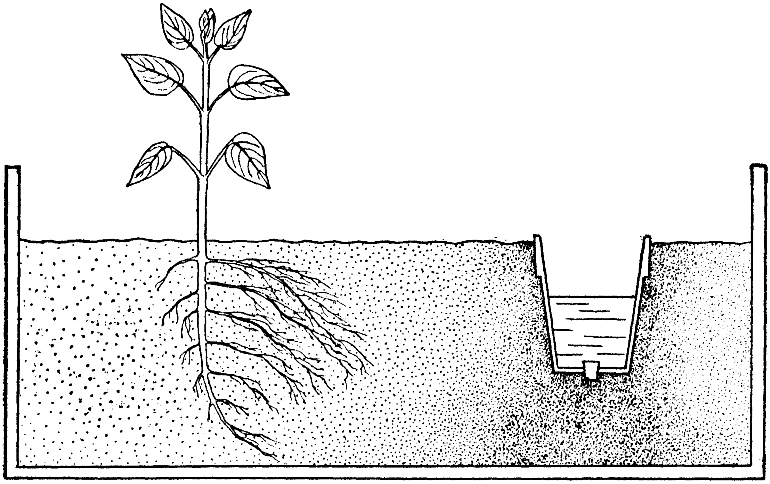


FIG. 129. Section of a box containing sand, with a plant near one end and a porous flower pot containing water near the other. The soil is moister near the pot, as indicated by the darker shading, and the unequal water content of the soil on different sides of the plant affects both the form and the direction of growth of the roots.

plants. The root systems of such plants are in general relatively extensive, sometimes reaching to great depths. Many cacti have widely spreading root systems, extending laterally rather than deeply into the soil. Roots of plants growing in swampy soil are often shorter than those of plants of the same species growing in drier habitats.

Water exerts an influence also upon the forms of aërial parts of plants, largely on account of differences in transpiration. Plants grown in damp air often have longer internodes and larger and thinner leaf blades than those of the same species grown in dry air. Leaf blades of nasturtiums growing in moist air and moist soil may be four or five times as large as those of nasturtiums living in dry air and dry soil. A frequent consequence of a change

from an aërial to an aquatic environment or *vice versa* is that certain organs, especially leaves, produced after the change differ in form from those previously produced. The leaves of the water crowfoot (Fig. 90) that develop in the air are very different in form and structure from those that develop under water.

111. Responses to the Presence of Other Substances. Substances other than water, such as oxygen, carbon dioxide, and illuminating gas in the air, or nutrient substances in the soil, may exert a formative as well as a directive influence upon plants. The presence of very small quantities of illuminating gas in the air of a greenhouse causes various abnormal developments and distortions of seedlings as well as the death of some plants. The direction of growth of roots is affected by the localized presence in the soil of mineral salts and other substances.

112. Responses to Mechanical Stimuli. The responses of plant organs to the various kinds of stimuli thus far discussed are generally visible only after the stimulus has been applied for some hours. The familiar sensitive plant, *Mimosa pudica,* a native of tropical South America, is especially suitable for the study of the immediate responses of entire organs to stimuli, particularly to those of a mechanical nature such as a touch or a blow.

Fig. 130. A sensitive plant (*Mimosa pudica*).

The plant (Fig. 130) has an erect, thorny, more or less branched stem. The leaves have long petioles and are compound, each having two to four primary leaflets which in turn bear numerous pairs of secondary leaflets.

If a single secondary leaflet of a Mimosa plant, under favorable conditions of light, moisture, and temperature, is touched very lightly, it reacts by bending upward and slightly toward the tip of the primary leaflet on which it is borne; if the stimulus is somewhat stronger, one or more pairs of secondary leaflets may fold together. If the stimulus is still stronger, there may follow a successive closure of each pair of secondary leaflets from the apex toward the base of the primary leaflet, and then a slight drooping of the primary leaflet. The secondary leaflets of the remaining primary leaflets may then close successively from base to apex, the primary leaflets droop somewhat, and the whole leaf droops. If the stimulus is very strong, its influence may be transmitted up and down the stem to other leaves and outward to their primary and secondary leaflets (Fig. 131). Some portions of a Mimosa plant are more sensitive than others to stimuli. The tips of secondary leaflets are very sensitive, but nearly all the epidermal cells of aërial organs, except parts of the flower cluster, are likewise sensitive to mechanical stimuli.

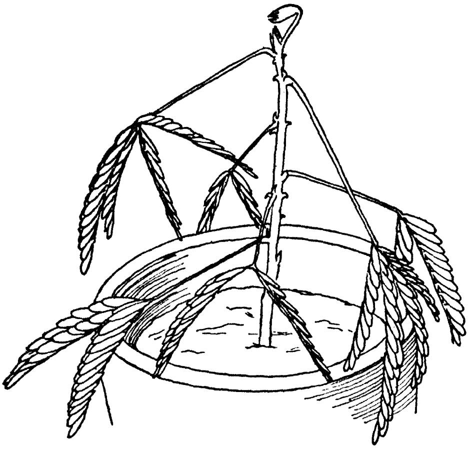


FIG. 131. A plant of Mimosa after leaflets and leaves have responded to a mechanical stimulus.

Unless a certain pressure is applied when a leaflet is touched, no change occurs in its position. That is, a certain intensity of the stimulus is necessary in order to produce a visible response; the stimulus must be sufficiently intense to bring about physical and chemical changes within the cells of the leaf.

The exact time interval between the application of a stimulus and the visible response can readily be determined. In Mimosa, the stimulus travels at the rate of from 8 to 20 mm. per second. The region in which the visible response occurs may be at a considerable distance from the region of perception of the stimulus.

This visible response, which consists in a bending of a leaf or of a leaflet, is due to the action of a motor organ, the *pulvinus*. There is a pulvinus at the base of each secondary leaflet, one at the base of each primary leaflet, and one at the base of the petiole (Fig. 132).

113. Structure and Action of a Pulvinus. A pulvinus is an enlargement at the base of a leaflet or of a petiole. In the center of

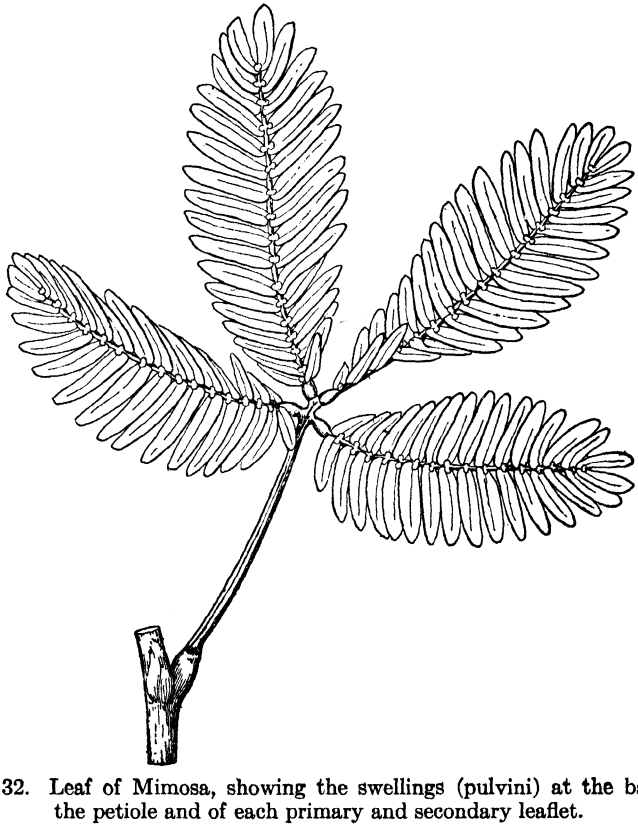


FIG. 132. Leaf of Mimosa, showing the swellings (pulvini) at the bases of the petiole and of each primary and secondary leaflet.

each pulvinus (Fig. 133) is a strand of vascular tissue, surrounded by a cylinder of living thin-walled cells; between these cells are fairly large intercellular spaces. When the effect of a stimulus has been transmitted to the pulvinus of the petiole, water exudes into the intercellular spaces from the thin-walled cells in the lower side of the pulvinus. These cells, therefore, lose their turgidity, and, since the turgidity of the cells in the upper side of the pulvinus is

not diminished, the petiole is bent downward. That the cells in the upper portion of the pulvinus take an active part in the movement is shown by the fact that the petiole is bent upward against the force of gravity when the plant is inverted and the leaf is stimulated. The pulvini at the bases of primary leaflets behave in essentially the same way as does the pulvinus of the petiole, but the pulvini of the secondary leaflets behave in the opposite way, in the sense that these leaflets are bent upward instead of downward when they are stimulated.

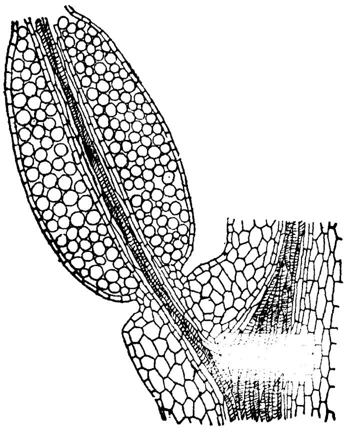


FIG. 133. Lengthwise section of a pulvinus (diagrammatic).

It is still uncertain exactly how the changes in permeability are brought about which result in a loss of water into the intercellular spaces from cells of a pulvinus. The stimulus will travel through a killed or girdled stem and is even transmitted through a severed stem if the two portions of the stem are connected by a glass tube filled with water. Some

FIG. 134. Oxalis plants; leaves in the characteristic positions by day (left) and by night (right).

evidence suggests that the reaction is caused by a substance originating in the stimulated cells, which travels in the xylem from the stimulated region to the pulvinus and there brings about changes in permeability.

114. "Sleep Movements." The same visible responses on the part of leaves and leaflets of Mimosa may be produced by other stimuli than that of contact. The change from light to darkness is a stimulus which causes the leaves and leaflets to change their positions. Leaves of many plants, including Mimosa and its relatives (peas, beans, alfalfa, clover, and other plants of the pulse family) as well as some members of other families, change their positions in late afternoon or evening (Fig. 134), thus reacting to variations in the degree of illumination. In the morning these

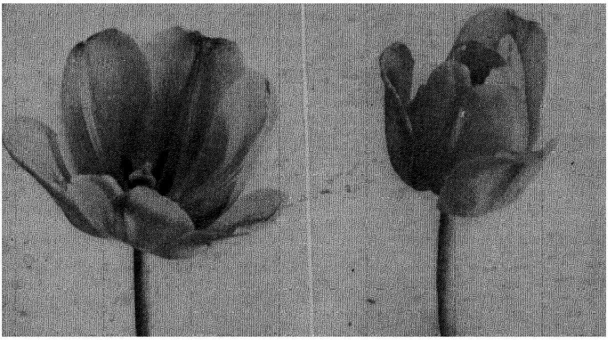


FIG. 135. The flower of a tulip, open during the day (left) and closed at night (right).

leaves return to the expanded position. The changes of position at the approach of night are often called "sleep movements," although they bear no relation to the sleep of animals. Other plant parts may respond to alternations of light and darkness; the flowers of many plants close at night and open in the morning. Such movements of floral parts, although induced by changes in illumination, are also influenced by temperature. Tulip and dandelion flowers may remain closed even on bright days if the temperature is sufficiently low. In plant parts possessing pulvini, such as leaves and leaflets, the movements, as has been seen, are due to changes in the turgidity of certain cells. The movements of floral parts, however, often result from inequalities of growth on opposite sides. For example, the opening of the sepals and petals of a tulip (Fig. 135) is due to a greater growth on their inner than on their outer sides. In the closing of these floral parts, growth is greater on their outer than on their inner sides.

115. Combined Effects of External Factors. Many influences are constantly acting upon every plant. An ordinary land plant has its roots imbedded in the soil while its stem grows in the air. Among the factors affecting the roots of such a plant are the size and the chemical composition of the soil particles; the amount and character of the soil water, which rains and other factors change from day to day and from season to season; and variations in temperature. The chemical and physical character of the soil is constantly changing, as well as its water content. The aërial portion of the plant is exposed to variations in temperature from hour to hour and from season to season; to variations in the duration of light and in its intensity; to variations in the amount of moisture, such as result from fogs, mists, rain, and snow; and to variations in many other factors. Thus the physical and chemical conditions prevailing in any particular region help to determine the type of plants found in that region. It is partly because conditions affecting the growth of plants vary at different parts of the earth's surface that the vegetation in each region differs more or less from that in any other region.

However, there are great differences between plants of different kinds in the nature and degree of their responses to environmental conditions. Under the conditions characteristic of any particular locality, some plants grow more rapidly than others, or grow to a greater size, or produce flowers and fruits more abundantly. The adaptations of plants to particular external conditions determine which species will thrive in any region and which will not. The characteristic appearance of the flora of any locality, then, is determined, first, by the type of plants that are adapted to life in that locality, and second, by the ways in which the responses of those plants to local conditions affect their forms and habits of growth.

CHAPTER XIII

THE CLASSIFICATION OF PLANTS

128. Bases of Classification. Thus far, plants have been considered from the standpoints of structure and of function without attempting to group them in an orderly manner. The earlier attempts of botanists to arrange plants in a system were entirely arbitrary and were based either upon the nature of the shoot, as the classification into trees, shrubs, and herbs, or upon a selection of certain floral features. Systems of classification based upon such arbitrarily selected characteristics are *artificial.* All present-day systems of classification are *natural:* that is, they attempt to indicate the actual relationships between plants of various kinds.

The grouping of plants according to relationship is based upon the conclusion that different plants have been evolved one from another; that is, that the kinds of plants now living are descended from common ancestors more or less remote. The evidence used in establishing the evolutionary relationships between plants is of varied nature; it is derived from: (*a*) the comparison of vegetative structures; (*b*) the comparison of reproductive structures; (*c*) the comparison of present-day plants with ancient plants (fossil plants); and (*d*) the study of the geographic distribution of plants now living. A more extensive discussion of the nature of this evidence will be found in Chapter XXXIII.

129. General Course of Evolution. A study of present-day plants shows, among other things, that it is possible for a single cell to live alone as an individual plant. A cell which so lives alone has, in a very general way, the same structure as one of the cells found in a complex, many-celled plant; but, considered as an organism, it is less specialized, since this one cell must perform all the functions that are carried on by all the cells of a many-celled plant.

All the available evidence indicates that the organisms which first appeared upon the earth were one-celled and that they lived in bodies of water. While these primitive organisms long ago disappeared, there are still many one-celled forms, some of which

are certainly very different from their early ancestors; but some of those now living seem to possess relatively primitive characteristics. Many one-celled organisms formed, and many still form, temporary associations known as *colonies*. Others acquired the habit of remaining together in more persistent colonies. In some persistently colonial organisms, as will appear in later chapters, a division of labor arose between different groups of cells, and these groups of cells became differentiated in ways that better fitted them to perform their particular functions. In this way tissues and organs appeared. In some lines of descent tissues became more varied and organs more highly specialized—that is, each organ, each tissue, and each cell was limited more and more narrowly as to the particular work that it might perform. Thus in a very general way the course of evolution has been from simple to more and more complex. However, it must not be overlooked that in many individual cases evolution has undoubtedly progressed in the opposite direction—that is, from a complex to a simpler organization.

The very first organisms, if they still existed, could not be classed either as plants or as animals. Many simple forms now living are likewise neither plants nor animals. Among one-celled organisms appeared some which, possessing chlorophyll and a cell wall, gave rise to the lines of descent which have led to the organisms that we call plants; whereas others, lacking a cell wall and lacking, or having lost, chlorophyll, became ancestors of what we know as animals.

In the course of time the habitation of some plants and animals was changed from water to land. Life on land presented new conditions, the adaptation to which led to the greater specialization of structures already present, as well as to the development of new tissues and organs. Hence, speaking very generally, the more complex and more highly specialized plants and animals live on land; the simpler ones, generally speaking, inhabit the water.

130. Genealogy of Plants. The evolution of plants might be represented by a line which branches early, and whose branches themselves repeatedly branch. If all the species of plants that have ever lived were fully known, their relationships could perhaps be shown by a diagram having the form of a much-branched tree. The root of this genealogical tree would be among the primitive one-celled forms among which the genealogical tree of animals

also arises; its highest branches would represent plants with the greatest complexity of structure. The branches would tend in all directions, including the downward one; for, as has been said, some plants have evolved from a complex to a simpler organization. The kinds of plants now living would be represented by the tips of some of the branches; and the task of one who studies the course of evolution is to reconstruct as large portions of this genealogical tree as the available knowledge of plants and of their relationships makes possible.

131. Classification. Those individual plants which are alike in most or all of their structural and functional characters constitute a *species.* The species is the unit used in classification. Different species which resemble each other closely are grouped together as a *genus.* Sometimes a genus includes but one species; more commonly it contains several or many species.

The botanical name of a plant consists of two words, the first denoting the genus, the second the species. For example, all sunflowers belong to the genus *Helianthus;* the commonly cultivated sunflowers constitute the species *annuus;* the name of the cultivated sunflowers therefore is *Helianthus annuus.* Similarly, the most widespread form of the water pest (Chap. II) belongs to the genus *Elodea* and the species *canadensis;* its name, therefore, is *Elodea canadensis.*

Just as species of plants are combined into genera, so genera in turn are grouped together in *families;* and families are combined to form successively *orders, classes,* and *divisions.* Following a widely used system of classification, all plants may be distributed among the following four divisions:

(*a*) *Thallophytes* are plants of relatively simple structure, not having stems, leaves, or roots like those of most ferns and seed plants. Thallophytes include *algae* and *fungi.* Typically, algae possess chlorophyll and can manufacture carbohydrates. Fungi lack chlorophyll and must obtain carbohydrates, and often other foods as well, from external sources.

(*b*) *Bryophytes* (liverworts and mosses). Members of this division lack vascular tissues. In some, the structure is as simple as that of many thallophytes; others are differentiated into stem and leaves. Bryophytes characteristically have many-celled reproductive organs, the outer layer of cells of each organ being sterile.

(*c*) *Pteridophytes* (ferns and their allies). A member of

division has a plant body containing vascular tissues. Pteridophytes, like bryophytes, have many-celled reproductive organs, the outer cell layer of each such organ being sterile.

(*d*) *Spermatophytes* (seed plants), which possess vascular tissues and which produce seeds.

In the succeeding chapters a few types representing each of these divisions will be discussed, as nearly as possible in their evolutionary order; that is, following the simpler forms, others will be considered approximately in the order of their increasing complexity. It must be borne in mind that, since most or all of the ancestors of any particular form to be studied have disappeared, such a selected series of types may show the *general course* that evolution has taken, but it can not show the detailed history of the evolution of any one species.

CHAPTER XIV

CHLOROPHYCEAE (GREEN ALGAE)

132. Nature. Members of this class have chloroplasts containing the pigments already mentioned (§ 85). Their carbohydrate food is stored usually in the form of starch. Most of them at some stage produce motile cells whose movement is brought about by slender, whiplash-like structures (*flagella*). The plant body (*thallus*) of a green alga may be a single cell or may be many-celled. In the latter case, its structure is of less complexity than is found in certain other classes of algae.

133. Distribution. Green algae, like other algae, are primarily aquatic and are widely distributed in both fresh and salt waters. Fresh-water members of the class occur in streams, lakes, and ponds. Some species grow attached to rocks and débris, some to larger plants. Others are unattached and constitute a large portion of the free-floating population of microscopic organisms known as *plankton*. At times the plankton algae of lakes and ponds are so numerous as to make the water appear colored. Such an abundance of plankton algae in reservoirs, followed by their death and decay, frequently gives rise to unpleasant tastes and odors which constitute a serious problem in connection with city water supplies. Green algae may grow also in places other than permanent bodies of water. They occur, for instance, in temporary pools, on moist, rocky cliffs, and on the shaded sides of trees and rocks. They grow on and in damp soils, where they sometimes develop so luxuriantly as to form a distinct layer. Certain species can live and multiply under conditions ordinarily thought of as unfavorable for the growth of plants. Examples of this nature are species living in brine lakes with a salt content of 15 to 30 per cent, and others which grow in the semi-permanent snow fields of arctic regions or of high mountains. Algae of the latter type may be so abundant as to cause a green or red coloration of the snow.

Many marine species live chiefly in shallow water along ocean shores, often being attached to rocks at levels that are exposed at low tide. Some attached forms, however, occur where the water is

as much as 300 to 600 feet in depth. Other marine algae are free-floating and constitute a part of the ocean plankton.

The green algae to be described in the present chapter are arranged approximately in their order of increasing complexity, either in structure or in methods of reproduction; but it must be borne in mind that the forms selected show only the general course of evolution within the class.

CHLAMYDOMONAS

134. Structure. *Chlamydomonas* is representative of the more primitive green algae. It occurs in ditches, pools, and lakes, or on moist soil. Sometimes it is found in such quantity that the water appears green; but many other minute algae may occur with Chlamydomonas and help to give the water a green or greenish appearance.

A cell of Chlamydomonas (Fig. 143, *A*) is typically egg-shaped. Like other cells that have been studied, it has a wall containing

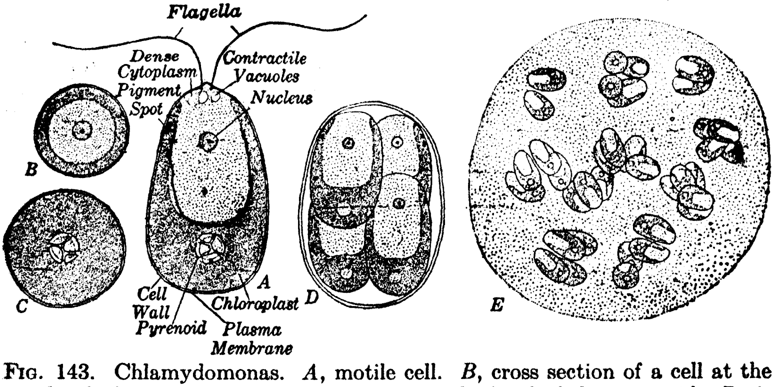


FIG. 143. Chlamydomonas. *A*, motile cell. *B*, cross section of a cell at the level of the nucleus. *C*, cross section at the level of the pyrenoid. *D*, 4-celled colony enclosed by the parent-cell wall. *E*, many-celled colony enclosed in a gelatinous matrix formed from the parent-cell wall.

cellulose. The most conspicuous portion of the protoplasm is the chloroplast. Each green cell of an Elodea or sunflower leaf contains numerous chloroplasts, but a Chlamydomonas cell has but one. This chloroplast, however, is large and very different in shape from the small, rounded chloroplasts that have been described. It looks somewhat like a horseshoe when viewed laterally; considered in three dimensions, it may be likened to a cup with very

thick bottom and sides. As in other cells, the film of the cytoplasm, lying just within the wall, is the plasma membrane. The chloroplast lies next within the plasma membrane. Imbedded in the center of the thicker, posterior part of the chloroplast is a small, colorless, spherical *pyrenoid*. The pyrenoid is a specialized portion of the chloroplast whose particular function is starch-formation. Treatment of the cell with iodine shows the presence of minute, variously shaped starch granules surrounding the pyrenoid. In fact, it is usually the zone of starch granules about the pyrenoid that is seen in a living cell, rather than the pyrenoid itself. The cell has no central vacuole, the central region inside the cup-shaped chloroplast being occupied by dense cytoplasm in which lies a small nucleus. It is a noteworthy fact that the nucleus of Chlamydomonas is similar, except for size, to a nucleus of one of the more complex plants. It has a membrane, nuclear sap, a nucleolus, and a chromatic network.

At the anterior end of the cell, two fine, thread-like extrusions of cytoplasm called *flagella* pass through the cell wall. Flagella are motile organs which, by lashing backward and forward, propel the cell through the water. The movement of the cell is not haphazard, but is a definitely directed response to stimuli. One stimulus largely affecting its movement is light, and the mechanism for the reception of light stimuli is localized in a small orange-red *pigment spot* near the anterior end of the cell. The effect of the light stimulus, received by the pigment spot, is transmitted to the flagella, causing them to move the cell in a definite direction. This response is usually positive, the cell swimming toward the light. If, however, the intensity of the light stimulus passes a certain point, the response is negative—that is, the plant swims away from the light. These responses can be shown by placing a dish containing many Chlamydomonas cells so that it is illuminated from only one side. In light of moderate intensity the cells collect as a green mass on the side of the dish toward the light (a positive response), but when placed in direct sunlight they frequently collect on the side away from the light (a negative response).

In the dense cytoplasm near the base of the flagella are a variable number (commonly two) of small transparent *contractile vacuoles*. The size of these vacuoles is not constant; they gradually expand to a certain size and then contract, thus extruding their contents. Their function seems to be that of excretory organs.

135. Reproduction. Sooner or later the cell ceases to move and draws in its flagella, and sometimes the wall becomes somewhat thicker. While the cell is in this quiescent state, it divides to form two daughter cells, both of which remain within the parent-cell wall. Cell division is preceded by a division of the nucleus, which goes on in substantially the manner described in Chapter XII. The division of the cell is by constriction.

This division of the parent cell is usually followed by another nuclear division, and this by a division of each of the daughter cells, forming four (Fig. 143, *D*); and in some cases there is a third division, resulting in the formation of eight cells. The cells so formed by division, whether two, four, or eight, remain for a time within the parent-cell wall and are not at first provided with independent walls. A group of cells so held together may be called a *colony;* but this colony of Chlamydomonas is but a temporary association. Sooner or later, each cell of the colony forms a wall of its own, produces flagella, and the parent-cell wall breaks down, allowing the young cells to become free. Each young cell is similar to the motile cell first described; and each, as it swims about, grows to approximately the size of the original cell.

Under certain environmental conditions the cells of a colony do not develop flagella and become motile, but remain within a matrix formed by a gelatinization of the parent-cell wall (Fig. 143, *E*). Since each of the cells may in turn grow, divide, and form daughter cells, a colony is produced consisting of numerous cells, sometimes as many as 100 or more, all enclosed within a single gelatinous matrix. Eventually the cells of such a colony form flagella and become free.

Thus, whatever the form of the resultant colony, it is during a quiescent stage in the life history of Chlamydomonas that an increase in the number of cells takes place. This increase in number is brought about by cell division. An increase in number of individuals is commonly spoken of as *reproduction.* In Chlamydomonas, therefore, as in all other one-celled organisms, reproduction and cell division are synonymous terms.

136. Gametes and Their Union (Fig. 144). Under some conditions the division of a quiescent cell and of its offspring continues until 16, 32, or 64 cells are formed. Except for their smaller size, the appearance of these cells is exactly like that of the motile cells described above; but their function is different, and they are called

gametes. The gametes are liberated by a dissolution of the parent-cell wall, and after swimming about for a time they come together in pairs. The cells of each pair are in contact at their anterior ends (Fig. 144, *C*). After two gametes have met, they begin to unite to form a single cell. The uniting gametes may be naked, or each may be surrounded by a wall. In the latter case the protoplasts escape from the walls, which are left behind and take no

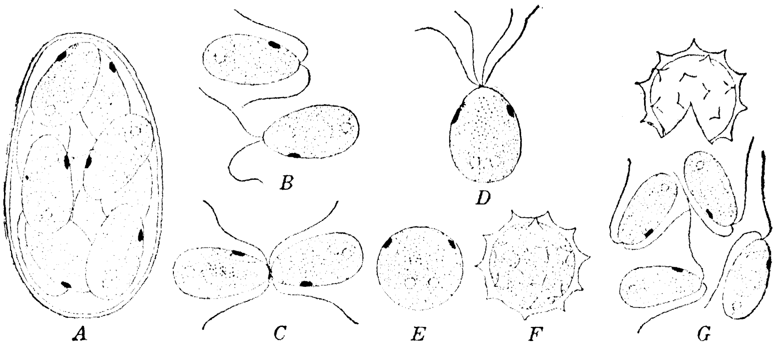


FIG. 144. Gametic union in Chlamydomonas. *A*, gametes before their liberation from the parent-cell wall. *B*, free-swimming gametes. *C*, early stage in the union of gametes. *D*, zygote, just after the union of the gametes. *E*, zygote, flagella withdrawn. *F*, mature zygote. *G*, germination of a zygote.

part in the process. In most species there is no visible difference between the two uniting gametes. However, in certain species, even though the gametes appear to be identical, union takes place only between two gametes which were produced by the division of different parent cells. Those species in which the gametes appear to be exactly alike represent the simplest type of gametic union.

The product of the union of two gametes is a *zygote* (Fig. 144, *D–F*). When first formed, the zygote has no wall and the two pigment spots, two chloroplasts, and two nuclei derived from the respective gametes are still present. The flagella may disappear during the union; or they may persist, the young zygote in the latter case being motile for a time. A motile zygote is readily distinguished from a motile vegetative cell or gamete by its possession of four flagella, as well as of two pigment spots and two chloroplasts. Sooner or later the flagella disappear, and the zygote becomes rounded and begins to secrete a thick wall. While this

wall is being formed, the two nuclei unite to form a single nucleus. The pigment spots, chloroplasts, and pyrenoids gradually become indistinguishable. In view of what is known of gametic unions in some other algae, it is probable that these bodies do not unite.

The zygote of Chlamydomonas is a resting cell. Its resistant wall is especially adapted to withstand unfavorable conditions, such as a drying up of the body of water in which the plant lives—a condition that would kill an ordinary motile cell. The contents of the zygote become red; the reserve starch disappears and is replaced by oil. Sooner or later, however, the protoplast of the zygote becomes green and divides, the daughter protoplasts divide, and each ultimate daughter cell, after developing flagella and a wall, is liberated by a rupture of the old wall of the zygote. The free-swimming daughter cells are then similar to the motile cells first described (Fig. 144, *G*).

137. Relationships. Chlamydomonas seems to be related on the one hand to a widely distributed class of one-celled aquatic organisms known as *flagellates*, and on the other to many or possibly all of the plants classed as green algae. The flagellates are commonly considered to be the relatively primitive group from which most classes of plants and of animals have descended. Chlamydomonas and the order (*Volvocales*) of which it is a member belong equally among the flagellates and among the green algae. As will be noted in later chapters, many of the so-called higher plants seem to have been derived through the green algae from flagellates like Chlamydomonas; others are probably independently descended from flagellates of different types.

138. Sexual Differentiation. Many simple algae and other one-celled or colonial organisms, including many flagellates, form no gametes so far as is known. However, the majority of organisms, both simple and complex, produce gametes which unite in pairs. The establishment of the habit of gametic union so early in evolutionary history, and its general persistence, suggest that the union of gametes may bear an important relation to the welfare of plant and animal species.

In such comparatively primitive organisms as Chlamydomonas, both gametes of any pair are motile and in most species are, so far as can be seen, alike in size and structure. But in various lines of

ber of whose cells is some multiple of two. In one of the most widely distributed of these (*Scenedesmus*, Fig. 148, *B–D*), the somewhat elongated cells lie side by side to form a row of 2, 4, 8, or 16 cells. In another genus (*Pediastrum*, Fig. 148, *A*), the cells are usually arranged in concentric rings to form a flat plate one cell in thickness. In both Scenedesmus and Pediastrum, any cell of a colony may, by a series of divisions, form a daughter colony.

Ulothrix

143. Structure and Reproduction. Many colonial green algae have an indefinite number of cells attached end to end in an unbranched row or filament. Such an alga is *Ulothrix* (Fig. 149),

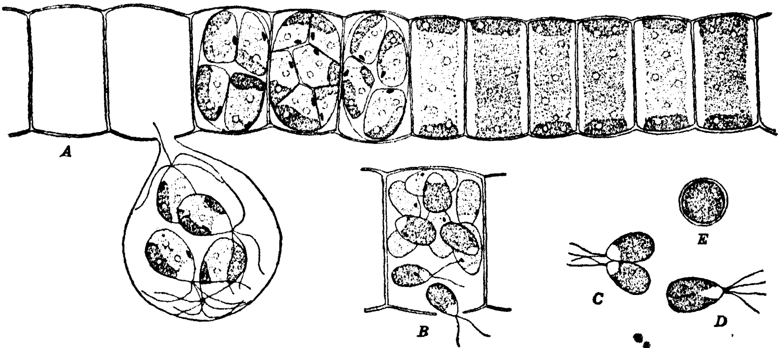


FIG. 149. Ulothrix. *A*, filament, some of whose cells have divided to form swarm-spores. *B*, liberation of gametes. *C*, *D*, union of gametes. *E*, mature zygote.

usually found attached to stones, sticks, or other objects in small, cool, swiftly flowing streams, or in pools or other bodies of water which do not become warm and stagnant. Each filamentous colony is commonly attached to the substrate by a disk-like holdfast developed from the basal cell. Sometimes colonies are free-floating. The cells are cylinders of very unequal lengths. Each cell contains a single chloroplast having the form of a partial or complete girdle imbedded in the peripheral part of the dense cytoplasm. The chloroplast contains one, two, or several pyrenoids. Near the center of the cell is a large nucleus.

Reproduction of cells takes place in Ulothrix, as in other plants, by means of cell division. The cells divide by constriction. Division increases the number of cells in the colony but not the number

of colonies. The number of colonies may be increased, however, by an accidental breaking of the filaments.

Reproduction of the colony (that is, the formation of new colonies) is brought about also by the production of motile cells (*swarm-spores*). With the exception of a few cells at the base, any cell of a filament may divide to form 2, 4, 8, 16, or 32 small naked cells. These daughter cells, at first angular, become rounded, form flagella, and, enclosed in a vesicle, escape through a pore in the side of the parent-cell wall (Fig. 149, *A*). These swarm-spores are similar to the motile cells of Chlamydomonas, each being ovoid and having a prominent chloroplast and a conspicuous pigment spot. Unlike the motile cells of Chlamydomonas, however, each swarm-spore has four flagella instead of two and is without a cell wall. After swimming for some time the spore comes to rest on some solid body, withdraws its flagella, forms a wall, and pushes out a protuberance which is the beginning of the formation of a holdfast. The growth and transverse division of this cell, of its daughter cells, and of their offspring, the cells always remaining in contact, give rise to a new filament. A cell of a colony may also, under some conditions, become an immobile rounded spore provided with a wall; or it may first divide to produce two or more such spores. A spore of this type may develop directly into a new filament, or may be transformed into a swarm-spore which will so develop.

144. Gametic Union. Ulothrix also produces gametes. These are formed in the same manner as are swarm-spores, and are similar to the latter except that they are frequently smaller and that each has two instead of four flagella (Fig. 149, *B*). After swimming for a time, the gametes unite in pairs (Fig. 149, *C–E*). In this union the flagella do not disappear, so that each zygote, having four flagella, continues moving about after its formation. Eventually it comes to rest, withdraws its flagella, secretes a wall, and, after a short period of rest, divides to form several (at least four) non-motile spores, each of which, like a swarm-spore, develops into a new filamentous colony.

145. Ulva. Certain green algae with cells similar to those of Ulothrix differ from that alga in the structure of their colonies. One of the most striking of these is *Ulva*, the "sea lettuce" (Fig. 150).

This plant commonly grows on rocks and wharves in brackish or salt water. The thallus, composed of Ulothrix-like cells, is an irregularly expanded sheet, often with a surface area of several square inches but only two cells in thickness. The plant is anchored at its basal end by a very irregularly shaped holdfast composed of elongated cells or rows of cells. Ulva produces four-flagellate swarm-spores and two-flagellate gametes.

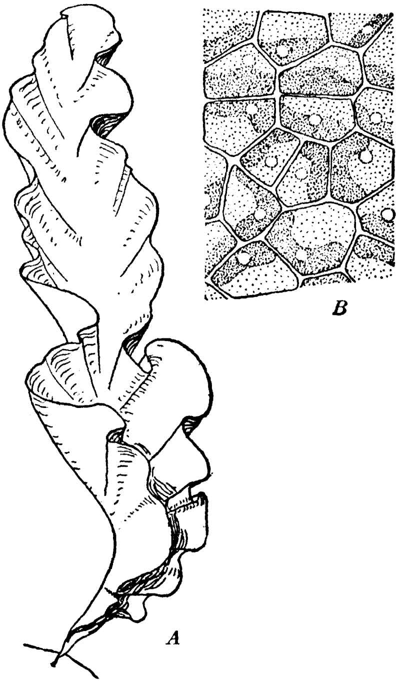


FIG. 150. Ulva. *A*, the expanded leaf-like thallus. *B*, portion of thallus, showing cell structure.

CLADOPHORA

146. Structure and Reproduction. Some filamentous green algae differ from Ulothrix both in cell structure and in colonial organization. An example is seen in *Cladophora* (Fig. 151, *A*), which grows attached to objects in streams and in shallow water along the shores of lakes. The cylindrical cells are united end to end to form a branching filament. Each cell is surrounded by a thick wall. Within the wall is a layer of dense cytoplasm in which are imbedded many small disk-shaped chloroplasts. Some chloroplasts contain one pyrenoid each, others lack pyrenoids. In some species the chloroplasts appear to be united into a continuous network. Cladophora differs from the algae previously described in that each cell contains many nuclei. These lie imbedded in the dense cytoplasm but farther inward than the chloroplasts.

Reproduction of cells is brought about through cell division by constriction. New branches are usually formed only by cells near the upper end of a filament. A branch originates as a lateral outgrowth from the upper end of a cell, and the first cross wall of the new branch is formed close to the point of origin of the outgrowth.

Reproduction of the colony results from the formation of one-nucleate, four-flagellate swarm-spores. These are produced by cells near the tips of branches, the protoplast of each such cell dividing to form many swarm-spores. The spores are liberated through a small pore near the upper end of the cell, or at its apex if it is the terminal cell of a branch. After swimming for a time a swarm-spore comes to rest upon some solid object, retracts its flagella, and secretes a wall. Growth and division of this cell, of its daughter cells, and of their descendants results in a new filament identical in appearance with that which produced the swarm-spores.

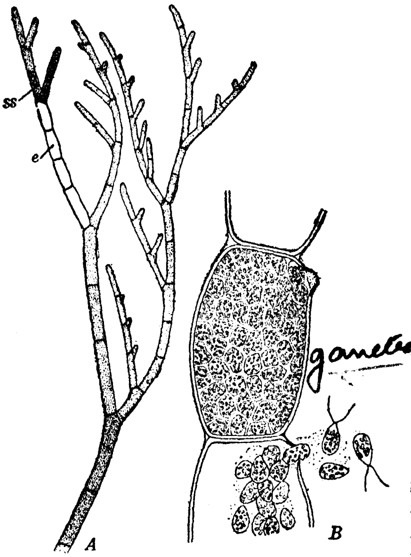


FIG. 151. Cladophora. *A*, portion of a plant; *ss*, cells dividing to form swarm-spores; *e*, empty walls from which swarm-spores have escaped. *B*, formation and liberation of gametes.

147. Gametic Union. Gametes are formed and liberated in the same manner as are swarm-spores, and are similar to the latter except that each has two instead of four flagella (Fig. 151, *B*). After swimming for a time, the gametes unite in pairs to form zygotes. A zygote becomes immobile and very soon secretes a wall. In some species the zygote develops immediately into a new filament which produces swarm-spores only.

148. Life Cycle. In the species of Cladophora last referred to, but apparently not in all species, the life cycle includes two distinct phases. Swarm-spores develop into plants which produce gametes. Each zygote formed by gametic union develops immediately into a plant exactly similar to that which formed the gametes; this plant, however, produces swarm-spores only. Since the spore-bearing plant (or generation) of Cladophora gives rise through spores to the gamete-bearing generation, and the latter generation through gametes and zygotes gives rise to the spore-bearing generation, there is an *alternation of generations.* In most

green algae there is no comparable alternation of generations, although a few others are known to have an alternation essentially similar to that just described.

SPIROGYRA

149. Structure and Reproduction. *Spirogyra,* one of the free-floating plants commonly known as "pond scums," is a green alga whose cells form permanent filamentous colonies. It occurs in pools and other bodies of water and frequently forms masses of considerable size. It may be distinguished from most other thread-like green algae by the slippery feeling of the threads, due to a gelatinous outer layer of the cell wall.

The cells of Spirogyra (Fig. 152, *A*) are cylindrical and attached end to end to form an unbranched thread. This arrangement results from the fact that all cell divisions take place in the same plane, namely, at right angles to the long axis of the cylindrical cells.

A thin layer of dense cytoplasm lies just within the wall of each cell. The most conspicuous feature of the cell, and the one from

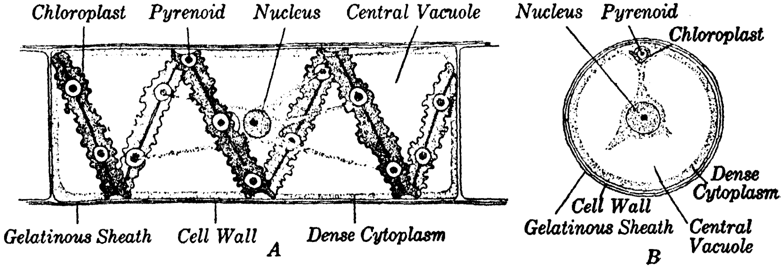


FIG. 152. *A*, cell of Spirogyra. *B*, cross section of a cell through the nucleus.

which the name *Spirogyra* is derived, is the chloroplast. Each chloroplast is a trough-shaped ribbon extending spirally from end to end of the cell; it is part of and contained in the dense cytoplasm. Each chloroplast contains several pyrenoids. Throughout the length of the chloroplast is a thick central strand connecting and surrounding the pyrenoids, the intervals between successive pyrenoids being approximately equal. A central vacuole occupies the greater portion of the space within the wall. In the center of this vacuole is the nucleus, surrounded by a layer of dense cytoplasm from which numerous cytoplasmic strands extend to the

dense cytoplasmic layer at the periphery of the cell. Each strand usually joins the peripheral layer just beneath a pyrenoid.

Reproduction of the cell takes place in Spirogyra in essentially the same manner as in other plants—that is, by means of cell division. Cell division in Spirogyra, under ordinary conditions, occurs at night. It is preceded by a nuclear division similar to that already described for the cells of a root tip. The division of the cells increases the number of cells in the colony but not the number of colonies. There is usually no definite means for reproduction of the colony—that is, an increase in number of colonies—during the vegetative life of the plant. In most species of Spirogyra new colonies are formed only when a filament is accidentally severed. Since various aquatic animals feed upon the alga, the filaments are frequently cut, so increasing the number of plants. In certain species of Spirogyra, especially in some with small cells, the filaments at times become separated into individual cells or short rows of a few cells each, which may then grow into long filaments.

150. Gametic Union. As a rule, the production of gametes by each species of Spirogyra occurs at a definite time of the year, commonly in spring or autumn. In preparation for this process the first step observed (in most species) is a pairing of the filaments so that the filaments of each pair lie side by side. Small dome-shaped protuberances now grow toward each other from opposite cells in the two filaments (Fig. 153, *A*, *B*), each protuberance increasing in size until it becomes a short tubular outgrowth. The outgrowths from opposite cells come into contact; the wall of each is digested at the point of contact, and thus a *conjugation tube* is formed. When the formation of the conjugation tube begins, the protoplasts (gametes) of the conjugating cells are similar in appearance, but as the protuberances grow toward each other, one of each pair of gametes contracts from the wall and becomes rounded. This change in size is brought about by a loss of water from the protoplast. The contracted gamete soon migrates through the conjugation tube (Fig. 153, *C*) toward the other, which at about this time also contracts and rounds up. The gamete which contracts first and which moves toward the other gamete is spoken of as *male* because of its greater activity; the passive gamete is *female*. Usually all the cells of a particular filament which function as gametes behave as gametes of the same sex, but at times some

of the cells in a filament become male and others in the same filament female gametes.

In certain species of Spirogyra, conjugation takes place between adjacent cells of the same filament rather than between cells of separate filaments. The differentiation into male and female gametes and the formation of a zygote go on, however, in the same way as when cells of different filaments conjugate.

After the male gamete has migrated into the cell cavity of the female gamete, the two unite to form a zygote (Fig. 153, *D–F*). Both a nuclear and a cytoplasmic union are involved. The cytoplasm of the gametes seems to become intermingled; but the

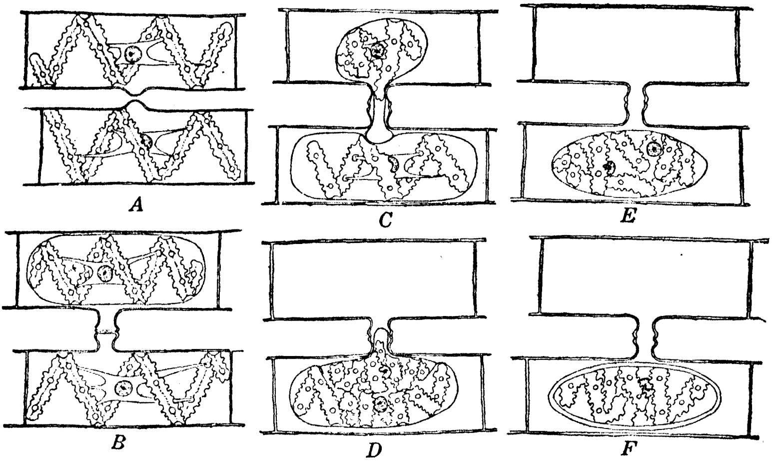


FIG. 153. Spirogyra; stages in the union of gametes and the maturing of a zygote (diagrammatic).

chloroplasts do not unite, those of each gamete remaining distinct for some time. The subsequent behavior of the chloroplasts is difficult to follow, but the available evidence indicates that the chloroplast or chloroplasts contributed by the male gamete disintegrate, so that the mature zygote contains only the chloroplast or chloroplasts derived from the female gamete. The zygote soon begins to secrete a wall which, when the nuclei have united and the paternal chloroplasts have disappeared, has become thick and resistant. By this time the zygote lies at the bottom of the pool or other body of water, still enclosed by the old wall of the female gamete. The zygote eventually becomes free, since both the wal

which enclosed the female gamete and the empty wall that formerly contained the male gamete disintegrate.

When a zygote is newly formed it contains the nuclei derived from the male and female gametes; these unite to form a single nucleus (Fig. 154, *A*, *B*). After a time this nucleus divides to form two daughter nuclei, and each daughter nucleus in turn divides (Fig. 154, *C–F*). The four nuclei now present in the zygote are similar when first formed, but three of them soon show signs of disintegration and eventually disappear. The fourth nucleus, however, persists and is the sole nucleus present in the mature zygote (Fig. 154, *G*, *H*). The significance of this behavior of nuclei in the zygote will become clear when certain corresponding processes in some of the more complex plants have been discussed (see Chap. XXV).

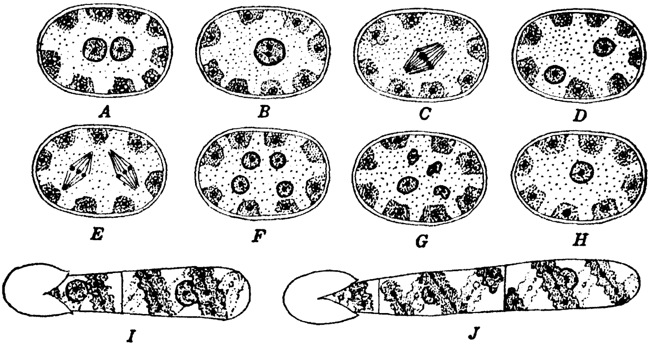


FIG. 154. Diagrams showing stages in the history of a zygote of Spirogyra; *A–H* in section; *I*, *J* in surface view. *A*, zygote just after the union of gametes; gamete nuclei still separate. *B*, male and female nuclei have united. *C*, first nuclear division in the zygote, forming 2 nuclei (*D*). *E*, second nuclear division, forming 4 nuclei (*F*). *G*, 3 nuclei beginning to disintegrate. *H*, after the disappearance of 3 nuclei. *I*, *J*, stages in the germination of a zygote.

151. Germination of a Zygote. After the union of the gametes, the color of the zygote contents changes from green to orange-red. Shortly before the zygote is to germinate, its contents again become green. The interval between the union of gametes and the germination of the zygote may be a few weeks or a few months, or it may extend from one spring until the next. In germination the heavy outer layer of the zygote wall is broken, and the cell contents, surrounded by the inner layer of the zygote wall, form a short

tubular outgrowth. The structures typical of a Spirogyra cell (chloroplast or chloroplasts, nucleus, and dense cytoplasm) are visible in this cell that lies partly within and partly without the broken portion of the wall of the zygote. A division of the nucleus is followed by a transverse division of the cell (Fig. 154, *I*). The daughter cell that is now partly within the zygote wall does not divide, but from the outer daughter cell a new filament is produced by repeated cell division and growth (Fig. 154, *J*). This filament is similar to the parent filaments.

When from any cause a cell that has prepared to function as a gamete does not unite with another, it not infrequently rounds up, secretes a thick wall, and so becomes, except for its somewhat smaller size, identical in appearance with a zygote. Such a resting cell (*spore*) can germinate in the same manner as a zygote to form a new filament. Thus it appears that any cell of a Spirogyra filament is capable of functioning either as a vegetative cell, as a spore which can grow into a new plant, or as a gamete.

Desmids

152. Structure. Almost every collection of algae from freshwater pools or lakes contains members of the group known as *desmids*.

It has been seen that the general course of evolution has been from simple to more complex forms. The filamentous colonies of Spirogyra and of Ulothrix represent, therefore, a more advanced as well as a more complex condition than does the one-celled Chlamydomonas. Desmids, on the other hand, are (chiefly) one-celled organisms whose immediate ancestors seem to have been filamentous algae closely related to Spirogyra. They illustrate, therefore, the possibility that evolution may at times be from complex to simpler, instead of from simple to more complex.

Most of the thousands of known species of desmids are distinguished from other one-celled green algae by a conspicuous median constriction, each cell thus consisting of two symmetrical half-cells (Fig. 155). The cells of various species differ greatly in shape and frequently bear spines or other protuberances. Each half-cell contains at least one chloroplast, often elaborately lobed, and within each chloroplast are one or more pyrenoids. A nucleus lies in the cytoplasm in the region of the median constriction.

153. Reproduction. New individuals are formed by the division of a parent cell into two daughter cells (Fig. 155, *G*). Before the cell divides the nucleus divides, each half-cell receiving a daughter

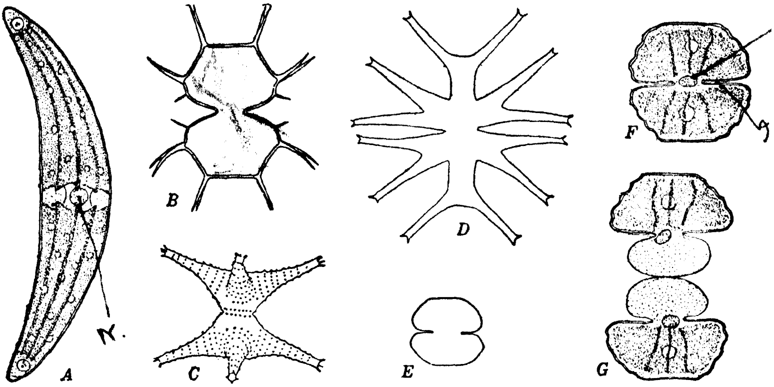


FIG. 155. Desmids. *A*, Closterium. *B*, Xanthidium. *C*, Staurastrum. *D*, Micrasterias. *E*, *F*, Cosmarium. *G*, division of a Cosmarium cell.

nucleus. Nuclear division is followed by a transverse division of the cell in the plane of the median constriction. Each daughter cell at first consists, therefore, of one half-cell and a portion of the

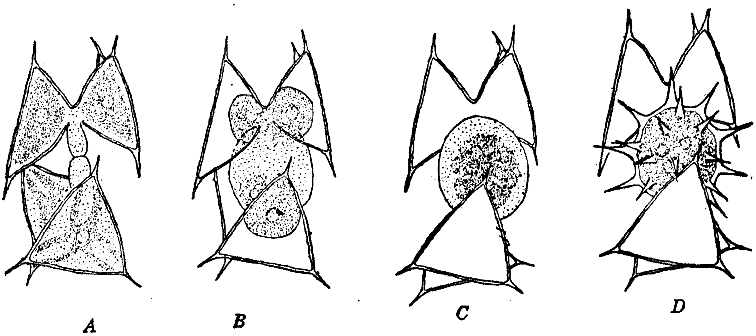


FIG. 156. Staurastrum; stages in the union of gametes. Adapted from De Bary.

median region of the parent cell. Later, by a growth of the constricted portion, each daughter cell develops a new half-cell. In most desmids the daughter cells become separated from each other as the new half-cells are forming, but in a few species the daughter cells remain united and by repeated division give rise to a filamentous colony.

154. Gametic Union. Occasionally, when two mature cells come to lie close to each other, their walls break at the median constrictions and their protoplasts function as gametes (Fig. 156), flowing out and uniting with each other to form a zygote. These non-flagellate gametes resemble those of Spirogyra except that they are not differentiated as male and female. When first formed the zygote is naked, but soon after its formation it secretes a thick wall. After a considerable period of rest the wall of the zygote breaks or becomes gelatinized and its contents develop into one, or (by division) into two or four vegetative cells of the form characteristic of the species.

OEDOGONIUM

155. Structure and Reproduction. *Oedogonium* is another unbranched filamentous green alga of frequent occurrence, at-

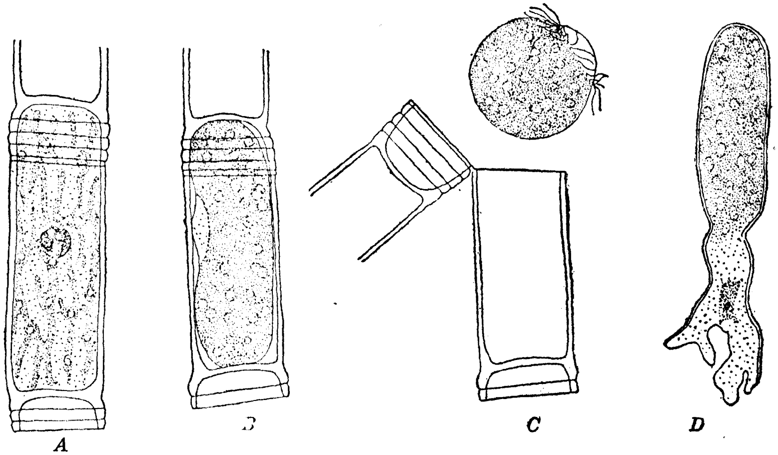


FIG. 157. Oedogonium. *A*, vegetative cell. *B*, swarm-spore before liberation. *C*, liberation of a swarm-spore. *D*, young plant produced by the germination of a swarm-spore. *B–D* after Hirn.

tached or forming floating masses in pools and other bodies of quiet water. The cylindrical cells (Fig. 157, *A*) are joined end to end. Inside the wall of each cell are a layer of dense cytoplasm containing a single chloroplast, a nucleus, and a large central vacuole. The chloroplast has the shape of a hollow cylinder with many irregularly shaped perforations. The large nucleus may lie toward one side of the cell, or may be suspended by cytoplasmic

strands in the middle of the central vacuole much as is the nucleus of Spirogyra.

Each cell of a filament may reproduce by division, the subsequent growth of the two daughter cells resulting, as in Spirogyra, in an increase in the length of the colony. As in Spirogyra, too, the number of colonies may be increased by an accidental breaking of the filament.

Reproduction of a colony occurs also through the formation of swarm-spores (Fig. 157, *B*, *C*). The protoplast of a cell withdraws somewhat from the wall, becomes rounded, and develops a colorless area at one side. A circle of flagella is developed at the margin of this colorless area. The protoplast has thus been metamorphosed into a swarm-spore. After the spore is mature, the old wall enclosing it splits transversely at one end, and the spore, moving slowly out through the opening in the wall, swims away by means of its flagella.

After swimming for some time, the spore comes to rest with its flagellate end in contact with some solid body, often a filament of Oedogonium. Soon the spore withdraws its flagella and secretes a wall, and its colorless end becomes modified into a disk-shaped or root-like holdfast. The cell now increases somewhat in length (Fig. 157, *D*) and then divides transversely into two daughter cells. The lower daughter cell, that with the holdfast, does not divide again; the upper cell by repeated transverse divisions gives rise to a long filament, which becomes free-floating if accidentally broken from its attachment.

156. Gametic Union (Fig. 158). Oedogonium forms gametes of two very different sorts. Any cell in a filament, except the basal cell, is capable of becoming an *oögonium*, but a cell which so develops is always one formed by a recent division. An oögonium becomes somewhat broader than a vegetative cell and spherical or ellipsoid in shape. Its protoplast (the female gamete or *egg*) shrinks and rounds up entirely within, and free from, the wall. As the egg approaches maturity, a small circular pore may be formed in the oögonial wall. In some species the wall cracks transversely instead of forming a pore. Since the oögonium and the egg are really the same cell, it is hardly necessary to apply both names in Oedogonium. But for the sake of harmonizing the use of terms in this and in some other algae in which an oögonium forms several eggs by division, it is customary to distinguish the egg of Oedo-

gonium, which is a protoplast only, from the oögonium, which is the protoplast plus the enclosing wall.

Simultaneously with the development of oögonia, certain other cells of the same or of another filament by repeated trans-

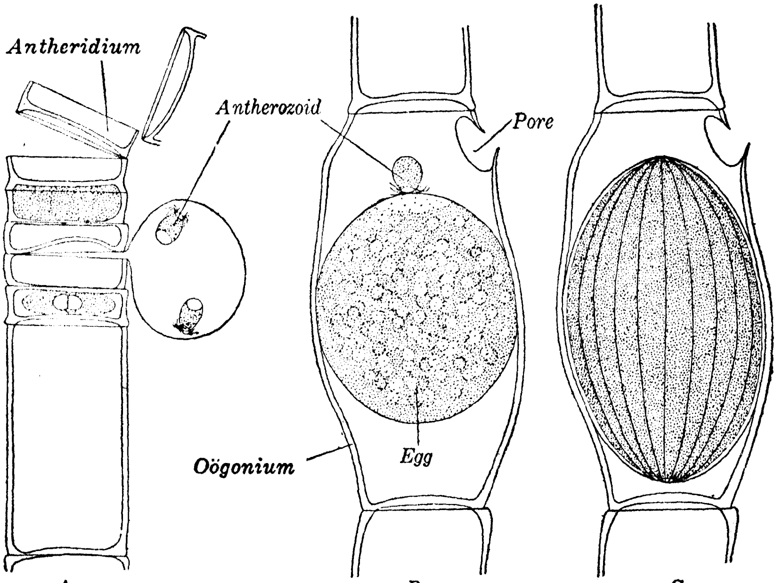


FIG. 158. Oedogonium. *A*, antheridia with antherozoids. *B*, oögonium in which an egg and an antherozoid are uniting. *C*, oögonium containing a mature zygote. After Hirn.

verse division form a short series of disk-shaped cells, each of which is an *antheridium*. The protoplast of each antheridium either becomes a male gamete (*antherozoid*) or divides to form two antherozoids. Except for their smaller size and their fewer flagella, antherozoids are similar in structure to swarm-spores. They are liberated from the walls enclosing them in the same manner as are swarm-spores. In certain species, antheridia are borne on very small, few-celled filaments which are attached to a filament bearing oögonia. An antherozoid swimming in the vicinity of an oögonium responds to a stimulus, exerted probably by a substance diffusing from the oögonium, swims through the pore or crack in the oögonial wall, and unites with the egg. The resultant zygote soon secretes a thick wall which often bears ridges, spines, or other protuberances.

The zygote is eventually liberated by the decay of the oögonial wall. After a period of dormancy it germinates (Fig. 159, *A*). The zygote wall breaks open and the protoplast by division forms four protoplasts (Fig. 159, *B*, *C*), each of which becomes a swarm-spore that may come to rest and develop into a new filament.

In the organization of its colony, Oedogonium represents no advance over Spirogyra or Ulothrix. However, in the marked

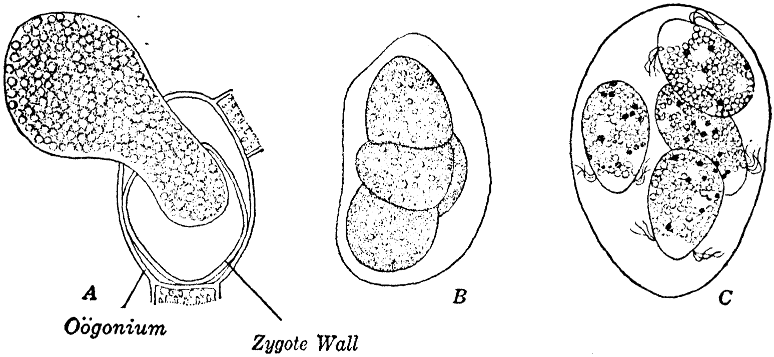


FIG. 159. Germination of the zygote of Oedogonium. After Juranyi.

differentiation of its gametes it presents a condition far in advance of that found in either Ulothrix or Spirogyra.

VAUCHERIA

157. Structure and Reproduction (Fig. 160). *Vaucheria* commonly forms a green, felt-like mass on damp soil or in shallow water. Each plant is a sparsely branched thread that may attain a length of several inches but consists of only a single cell. Within the wall of this cell is a layer of dense cytoplasm containing small flattened, rounded chloroplasts. Imbedded in the dense cytoplasm are numerous nuclei. A noteworthy feature of the chloroplasts of Vaucheria is the absence of pyrenoids and of their accompanying starch granules, the reserve food being stored in the form of oil droplets. The central vacuole constitutes the greater part of the volume of the plant.

A large swarm-spore is produced by a cell division near the end of a filament, followed by a rounding up of the portion of the protoplasm so cut off. Such a spore contains many nuclei and chloroplasts. Shortly before its liberation by a breaking of the

cell wall, a pair of flagella are developed opposite each nucleus, so that the freed swarm-spore bears numerous flagella. After swimming for a time the spore comes to rest, withdraws its flagella,

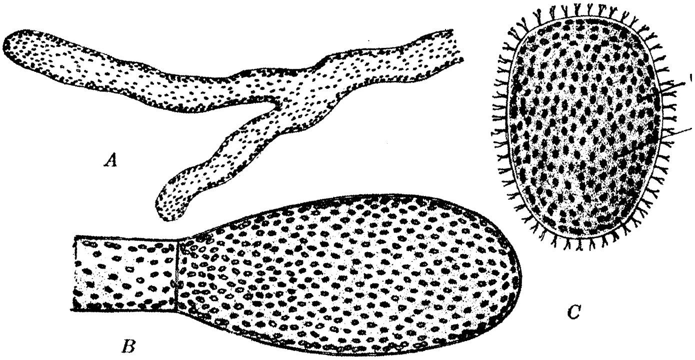


FIG. 160. Vaucheria. *A*, portion of a plant. *B*, end of a branch, showing the formation of a swarm-spore. *C*, swarm-spore after its liberation.

and grows into a new plant. Under certain conditions the spore does not form flagella. However, when such a non-motile spore

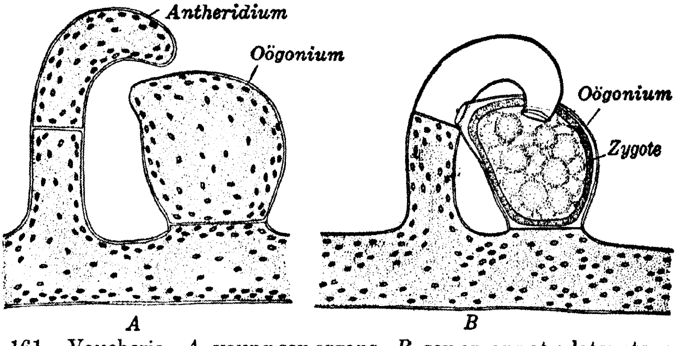


FIG. 161. Vaucheria. *A*, young sex organs. *B*, sex organs at a later stage; the antheridium empty, the oögonium containing a zygote.

becomes separated from the plant which produced it, it develops into a new plant in the same manner as does a swarm-spore.

158. Gametic Union (Fig. 161). The gametes of Vaucheria are differentiated as male and female. The male gametes (*antherozoids*) are produced within an *antheridium* which is at first a small terminal cell cut off by a cell division in a short curved branch. A young antheridium contains many nuclei and chloro-

plasts, but later the chloroplasts disappear. Eventually the protoplast of the antheridium is divided into a number of one-nucleate antherozoids which are liberated by a dissolution of the wall at the apex of the antheridium. Each antherozoid is small and spindle-shaped, lacks a wall, and has two lateral flagella.

The female gametes (*eggs*) are borne in *oögonia*. Each oögonium in some species is borne on the same branch that bears an antheridium; the oögonia of other species are borne on separate branches that arise near the antheridial branches. Like an antheridium, an oögonium is the end of a branch separated by a cell division and the formation of a cross wall. At first the young oögonium contains several nuclei, only one of which, however, persists; the protoplast of the oögonium, which includes the persistent nucleus, is now the egg. As the oögonium matures, a beak-like protuberance develops at one side and the wall disintegrates at this point. The antherozoids, which are liberated at this time, enter the oögonium through the opening, and one antherozoid unites with the egg. After this union the zygote develops a thick wall. It is eventually liberated by a disintegration of the oögonial wall and, after a longer or shorter period of rest, develops directly into a new filamentous plant.

159. Sexual Differentiation. The green algae discussed in the present chapter illustrate several stages in the development of differences between gametes. Most species of Chlamydomonas form gametes that are visibly alike in all respects. The same is true of Ulothrix, although this alga has advanced much beyond Chlamydomonas in its colonial organization. In Spirogyra, the gametes have become differentiated with respect to motility, but are not greatly different in other ways. In Volvox, Oedogonium, and Vaucheria, male and female gametes have come to be very different in size, structure, and behavior. Since Spirogyra, Volvox, Oedogonium, and Vaucheria represent distinct lines of descent, it appears that sexual differentiation has proceeded on parallel courses in various independent lines.

CHAPTER XV

MYXOPHYCEAE (BLUE-GREEN ALGAE)

160. Nature. The members of this class contain a blue pigment, in addition to chlorophyll and the accompanying yellow pigments. Although the presence of blue, green, and yellow pigments typically gives the organisms a blue-green color, variations in the proportions of these pigments cause the appearance of many shades and colors such as yellow, orange, pink, red, violet, purple, brown, and black. A preponderance of carotin, for example, results in a yellow or reddish color. Blue-green algae differ from green, brown, and red algae also in the absence of definite plastids, in the organization of their nuclear substance, and in the complete lack of swarm-spores and gametes.

Although included among the thallophytes, the blue-green algae are to be regarded as a class of this division of the plant kingdom that is not closely related to the other classes, and one which has probably arisen independently.

161. Distribution. Blue-green algae are widely distributed in both fresh and salt water. Fresh-water blue-green algae are of common occurrence in pools and ditches, especially in those containing stagnant water. Many of the plankton algae of fresh-water lakes and reservoirs are members of this class, and blue-green algae are chief among the organisms whose decay sometimes causes disagreeable odors and tastes in water supplies. The water of the Red Sea is at times colored by the presence of immense numbers of colonies of a species belonging to this class.

These algae are prominent also among those which grow on damp soil and form papery layers on the surface of the earth. Almost all the algae of hot springs are blue-greens. Among the best-known instances of their occurrence in hot springs are in those of Yellowstone National Park. The brightly colored terraces of these springs result from a deposition by the algae of mineral substances dissolved in the spring waters.

162. Gloeocapsa. The cells of certain genera of blue-green algae are solitary; those of other genera are united in colonies of

definite or indefinite form. *Gloeocapsa* (Fig. 162) is a one-celled member of the class. Its solitary cells are spherical, each being surrounded by a thick gelatinous sheath which is often stratified. Frequently two or more daughter cells of Gloeocapsa remain within the sheath of the parent cell, forming a more or less persistent colony.

Within the thin wall of each cell is a protoplast, differentiated into an outer colored and an inner colorless region. The colored

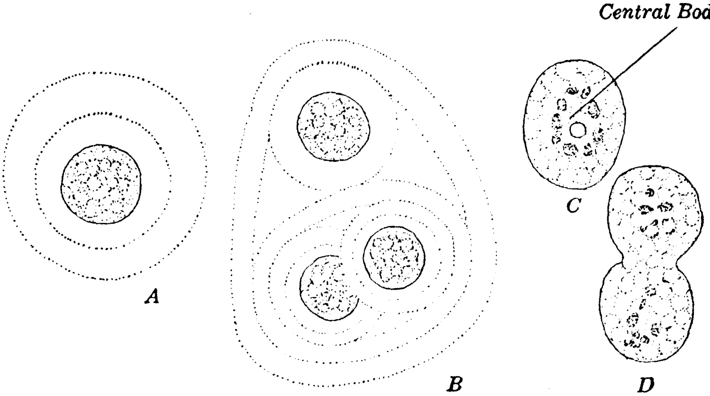


FIG. 162. Gloeocapsa. *A*, single cell. *B*, 3-celled colony. *C*, cell killed and so stained as to show the central body. *D*, dividing cell. *C*, *D* redrawn from Olive.

portion of the protoplast contains the pigments already mentioned. The pigments appear to be evenly distributed throughout the peripheral portion of the protoplasm rather than located in definite plastids. In the colored region of the protoplasm are also colorless granules, some of which are reserve foods. Probably many of these are composed of *glycogen*, a carbohydrate somewhat similar to starch. In the central colorless region of the cell is a relatively dense mass of material, the *central body*. This body is described by some observers as consisting in part of substances of the nature of those composing chromosomes, being therefore a nucleus of primitive type but without a nucleolus or a nuclear membrane. Other investigators question this conception and hold that a definite nucleus is lacking. The material of the central body, however, takes the same stains as do chromosomes, and is commonly considered to correspond in some measure to the substance of a true nucleus.

An increase in number of cells is brought about in Gloeocapsa, as in other algae, by cell division (Fig. 162, *D*). Before dividing, a cell elongates somewhat and the chromatic substance of its central body becomes divided into two masses. The cell is then divided transversely by a constriction of the plasma membrane, and each daughter cell becomes rounded and secretes a new gelatinous sheath.

163. Some Colonial Blue-green Algae. There are a considerable number of blue-green algae whose spherical cells are enclosed in a common gelatinous matrix. Cell division in these colonial algae may be in two or in three planes. In the former case, as in *Merismopedia* (Fig. 163, *A*), the result is a flat, plate-like colony. Cell division in three planes results in a more or less massive colony, as in *Coelosphaerium* (Fig. 163, *B*) and *Aphanocapsa* (Fig. 163, *C*). Reproduction of the colony results from its accidental rupture, or from the occasional freeing of a cell which then by division develops into a new colony.

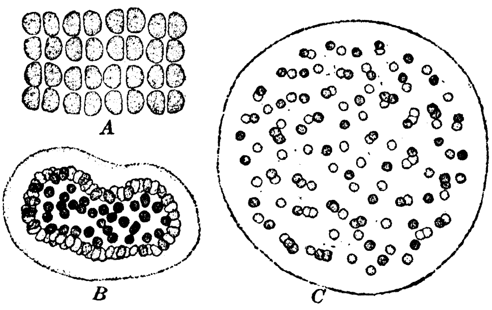


FIG. 163. Colonial blue-green algae. *A*, Merismopedia. *B*, Coelosphaerium. *C*, Aphanocapsa.

164. Oscillatoria. In the majority of colonial blue-green algae, cell division is always in the same plane. The result is a simple

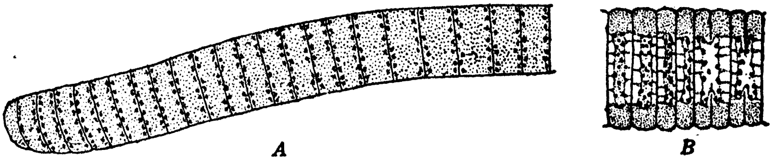


FIG. 164. Oscillatoria. *A*, portion of a living filament. *B*, cells killed and stained, showing the central body. *B* redrawn from Olive.

unbranched row or filament of cells. One of the commonest filamentous forms is *Oscillatoria* (Fig. 164), which is often abundant in temporary pools or on damp soils.

At each end of a filament of Oscillatoria is a hemispherical or

conical cell whose free end is frequently expanded to form a button-like cap. The other cells of the filament are disk-shaped or cylindrical. Each cell is surrounded by a wall. The protoplast, like that of Gloeocapsa, is differentiated into a colorless central region and a colored outer portion. A feature which distinguishes Oscillatoria from other blue-green algae, and which suggested its name, is its oscillating movement. A filament frequently waves back and forth, and occasionally moves longitudinally a short distance. The mechanism of these movements is unknown.

As in other filamentous algae the number of cells in a filament is increased by cell division, the central body dividing before, or at the same time as, the cell divides. Oscillatoria has a definite means also of bringing about the reproduction of filaments. Frequently gelatinous disks are formed between adjacent cells at certain points in a filament; later the filament breaks at these points into several short parts each composed of a few cells, which may then, by division and growth, develop into longer filaments.

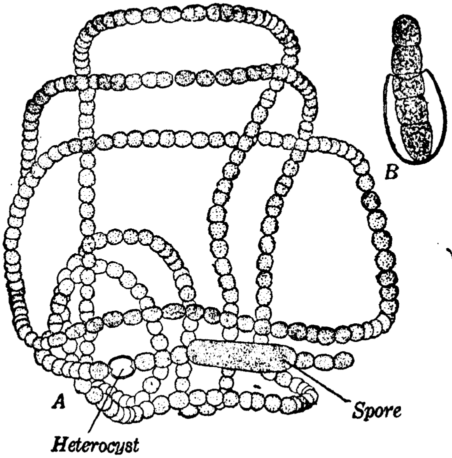


FIG. 165. *A*, filament of Anabaena with a spore and a heterocyst. *B*, development of a spore of Cylindrospermum into a new filament.

165. Anabaena. Another filamentous blue-green alga of frequent occurrence in pools, ditches, and the plankton of fresh-water lakes is *Anabaena* (Fig. 165, *A*). The cells of Anabaena are spherical and attached to one another so as to appear like beads in a necklace. The filaments may be straight or very much bent and contorted. Surrounding each filament is a thick, very transparent gelatinous sheath. The cells have much the same structure as those of Gloeocapsa or of Oscillatoria.

An occasional cell of an Anabaena filament enlarges greatly, becomes filled with reserve foods, and develops a thicker wall.

Such a *spore* eventually becomes separated from the parent filament and may develop into a new colony (Fig. 165, *B*).

Here and there in a filament are cells with much thicker walls and with transparent contents. These are *heterocysts*. Heterocysts are spore-like in nature, but they are spores whose capacity to develop into new colonies has been almost completely lost. The filaments of some blue-green algae having heterocysts regularly break into shorter filaments at the points where the heterocysts occur; but this is not so generally the case in Anabaena.

166. Nostoc. Other filamentous blue-green algae with heterocysts differ from Anabaena in the shape of the colony or in the

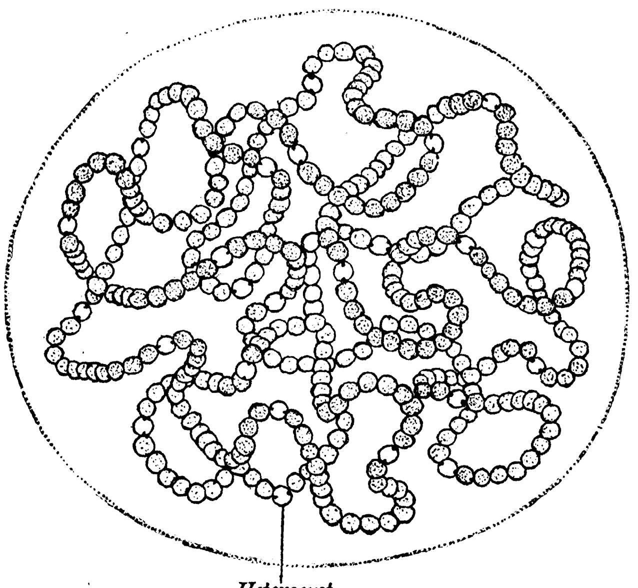


FIG. 166. Colony of Nostoc.

arrangement of their cells. *Nostoc* (Fig. 166), which grows both on damp soils and in water, resembles Anabaena in cell and colonial structure and in spore-formation. A Nostoc colony is surrounded by a gelatinous sheath much firmer and tougher than that of Anabaena.

A colony of Nostoc may become separated into daughter col-

onies which remain within the original tough sheath. By the growth and breaking of the daughter colonies a mass of considerable size is often formed. Such a mass contains numerous filaments imbedded in a gelatinous matrix, and may be considered a compound colony.

CHAPTER XVI

PHAEOPHYCEAE (BROWN ALGAE)

167. Nature. The brown algae are almost exclusively marine and are most abundant along the shores of colder portions of the oceans. Their cells contain golden-brown plastids which owe their color to a pigment chemically similar to carotin, that masks the chlorophyll which is likewise present. Brown algae are distinguished from algae of other classes also by the structure of their swarm-spores and motile gametes. For this reason, particularly, the brown algae are considered not to be directly related to the green algae, but in all probability to have arisen from unicellular flagellates very different in structure from Chlamydomonas.

Evolution within the class of brown algae has produced plants with much greater complexity of external form than has been attained by any of the green algae mentioned in an earlier chapter. Many brown algae have developed also a considerable degree of tissue-differentiation, and some grow to a very large size. Although in size and in complexity of structure some of them are fairly comparable with many seed plants, brown algae are to be included among the thallophytes because of their simple spore- and gamete-producing organs.

ECTOCARPUS

168. Structure and Spore-formation. *Ectocarpus* (Fig. 167, *A*) has a much-branched filamentous thallus which grows attached to stones, rocks, and other objects, particularly those that are exposed by tidal action. The cells are cylindrical. Within each cell wall is a one-nucleate protoplast containing numerous small golden-brown plastids.

In some plants, terminal cells of the main branches, or the terminal cells of short lateral branches, develop into *sporangia* (Fig. 167, *B*). A sporangium begins its development as a one-nucleate cell with numerous plastids. After a series of nuclear divisions its protoplast becomes divided into swarm-spores which are liberated by a breaking or dissolution of the wall at the upper

end of the sporangium. Each spore (Fig. 167, *C*) is pear-shaped, has one nucleus and one plastid, and bears two lateral flagella of unequal length. After swimming for a time the spore comes to rest and develops into a new plant.

169. Gametic Union. Other plants of Ectocarpus produce gametes. These are formed in multicellular organs (sex organs)

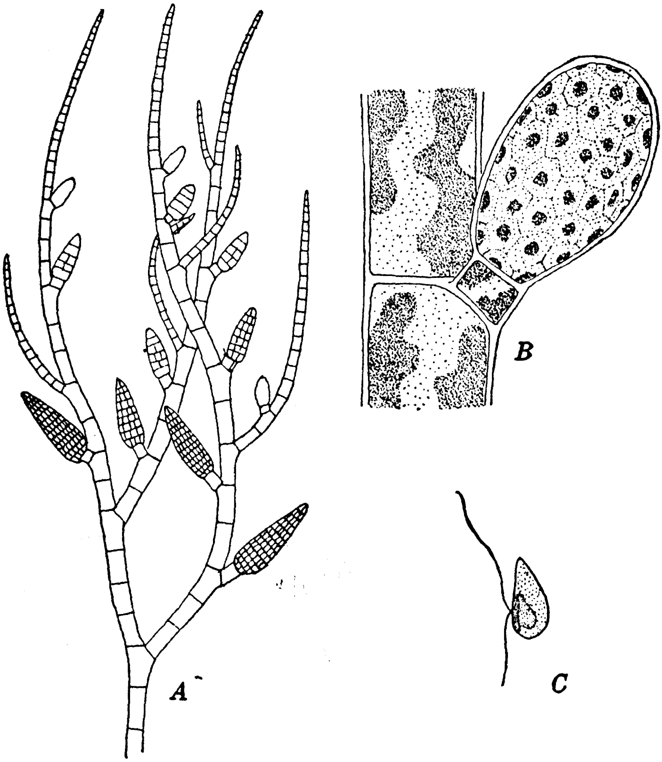


FIG. 167. Ectocarpus. *A*, portion of a thallus bearing sex organs. *B*, sporangium. *C*, swarm-spore.

which, like sporangia, are terminal in position. Each of these organs consists, unlike a sporangium, of many transverse layers of small cubical cells separated by walls (Figs. 167, *A*; 168, *A*). The protoplast of each cell is metamorphosed into a motile gamete which is liberated by a breaking of its enclosing wall. The gametes (Fig. 168, *B*) are similar to, though usually smaller than, the swarm-spores, and they are capable, under favorable conditions,

of uniting in pairs to form zygotes (Fig. 168, *C–F*). Before their union occurs some of the gametes become motionless. These are considered female gametes. Other (male) gametes remain active. One male gamete unites with each female gamete. If conditions are not favorable to their union, the gametes of Ectocarpus, like those of Spirogyra, may function as spores, developing directly into new plants.

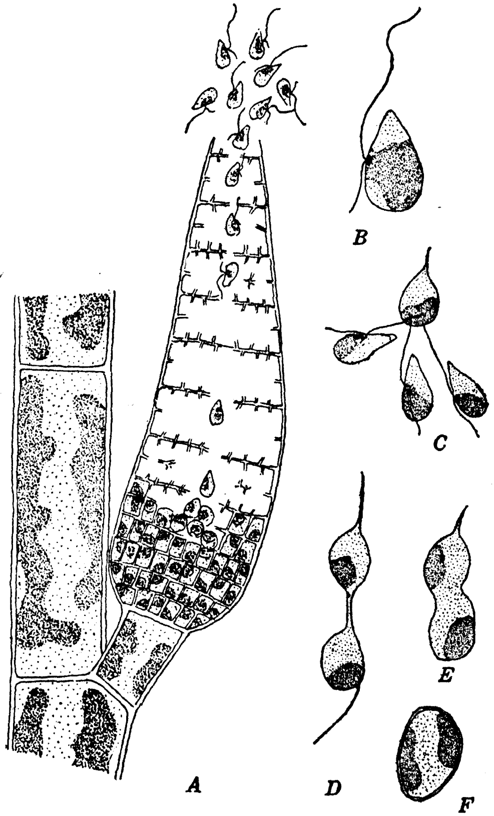


FIG. 168. Ectocarpus. *A*, sex organ, gametes being liberated. *B*, gamete. *C*, female gamete (above) whose flagella have been withdrawn; below, 3 male gametes. *D*, *E*, stages in the union of gametes. *F*, zygote. *B–F* redrawn from Berthold.

LAMINARIA

170. Structure. *Laminaria,* the common kelp, grows in comparatively shallow water near rocky ocean shores but just below the lower tide level. Like other large brown algae, it is most abundant in relatively cool waters. At one time kelps and rockweeds (§ 174) were of considerable importance as sources of potassium and iodine. The discovery of mineral deposits containing these elements has, however, made their recovery from algae unprofitable.

A plant (Fig. 169, *A*), which may be six feet or more in length, is attached to the rock by a holdfast that superficially resembles a much-branched root system. Above the holdfast is a short central axis which is continuous with a large flattened blade; in

certain species the blade is divided lengthwise into several segments. The central axis consists of a tough outer cortical zone and a loose inner region. The blade, likewise, has compactly arranged cells next the surface and loosely arranged cells in the interior.

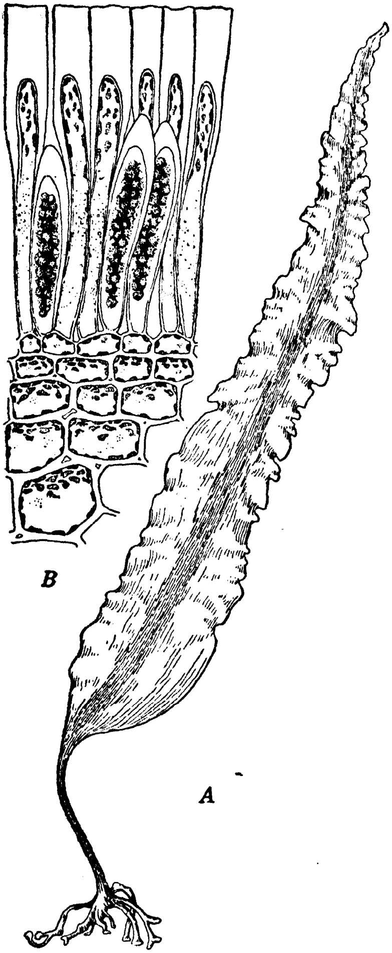


FIG. 169. Laminaria. *A*, thallus. *B*, cross section of a portion of a thallus bearing sporangia. *B* after Oltmanns.

171. Reproduction. During certain seasons of the year some of the surface cells of the blade of Laminaria develop into sporangia which are very similar in structure and development to the sporangia of Ectocarpus. The sporangia of Laminaria occur in closely packed groups in the blade, intermingled with elongated hair-like cells (Fig. 169, *B*). The swarm-spores, similar in appearance to those of Ectocarpus, are liberated by a breaking of the sporangial walls.

Contrary to what might be expected, a swarm-spore develops, not into a plant similar to that which formed it, but into a very small branched filamentous plant. Furthermore, the plants that develop from swarm-spores are of two sorts, producing respectively female and male sex organs. The male plants (Fig. 170, *A*) bear many small antheridia near the tips of their branches. The protoplast of each antheridium becomes a motile antherozoid. On female plants (Fig. 170, *B*) oögonia are developed, usually from terminal cells but sometimes from other cells of the branches. An oögonium is longer and thicker than other cells of the plant; its protoplast

becomes an egg containing numerous plastids. The mature egg is extruded through, and remains attached to, the tip of the oögonium.

After an antherozoid has united with an egg the resultant zygote divides transversely. Further transverse divisions produce a short

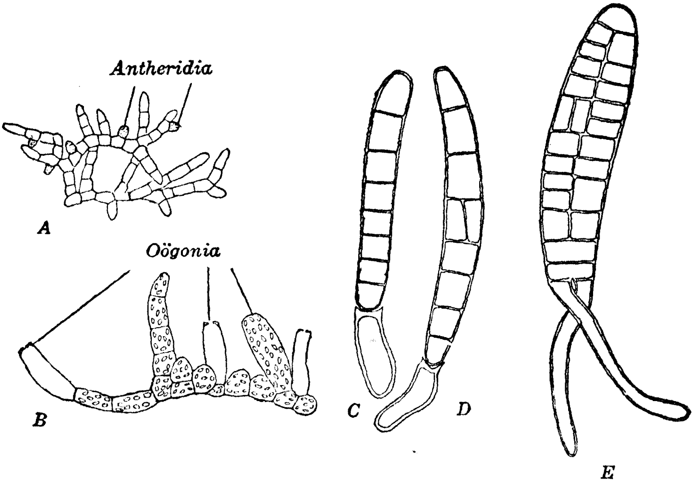


FIG. 170. Laminaria. *A*, male plant. *B*, female plant. *C–E*, young plants produced by the germination of zygotes. *A* and *B* redrawn from Miss Myers: *C–E* redrawn from Kylin.

filament of 6 to 10 cells (Fig. 170, *C*, *D*). Later divisions are in three planes, and continued growth and division lead to the development of a mature plant like that first described, with holdfast, central axis, and blade. Under certain conditions an egg may develop into a new plant without uniting with an antherozoid.

172. Life Cycle. There are two distinct phases in the history of Laminaria. Swarm-spores develop into small filamentous plants which produce gametes. The union of gametes results in the formation of a zygote, from which develops a large plant that produces spores. Since the gamete-bearing plant (or generation) of Laminaria gives rise through the zygote to the spore-bearing generation, and this generation through the spores gives rise to the gamete-bearing generation, Laminaria has an *alternation of generations.*

A similar alternation of generations appears to characterize other genera of the brown algae. It is probable that the union of

gametes in Ectocarpus (at least in some species) produces zygotes which develop into spore-bearing plants; and that the spore-bearing plants, in turn, give rise, through the spores, to gamete-bearing plants. If this is true, the two generations of Ectocarpus are identical in appearance, except for their reproductive structures; in Laminaria, on the contrary, the two generations are very different in size and structure.

173. Other Kelps. Many of the kelps of the Pacific coast are notable both for their complexity of external form and for their habits of growth. One of the most remarkable is *Postelsia* (the "sea palm," Fig. 171), which grows only at the water line on rocks exposed to the full pounding of the surf. This alga has a much-branched holdfast which anchors it firmly to the rocks, and a stout, flexible axis a foot or more in length, bearing at its apex a crown of leaf-like blades.

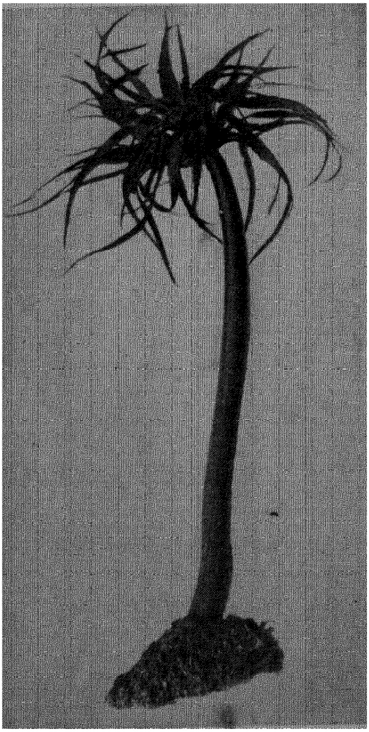


FIG. 171. The "sea palm," Postelsia. Photograph by Lewis Josselyn.

Many of the "giant kelps" of the Pacific coast are annuals, and some of them grow to a length of 100 feet or more in a single season. *Nereocystis* (Fig. 172), one of these giant kelps, grows in water 20 to 40 feet in depth. It is anchored to the rocky bottom by a holdfast from which arises a long, slender axis. The upper portion of the axis is expanded to constitute a gas bladder that floats on the surface of the water and bears several long, strap-shaped blades. Another giant kelp (*Macrocystis*), growing in similar locations, bears many small blades along its branching axis and a gas bladder at the base of each blade.

Fucus

174. Structure. The rockweed (*Fucus*, Fig. 174, *A*) is a common inhabitant of the sea coasts of all temperate regions. This alga grows most abundantly in the upper limits of the areas that are temporarily exposed by the tides. The leathery, flat, ribbon-shaped thallus is attached to rocks by the development of its basal end into a holdfast. The thallus forks at intervals, the two prongs of each fork being usually of the same length. Here and there along the thallus in certain species are large hollow, bladder-like expansions containing gases, chiefly carbon dioxide, that help buoy the plant when it is submerged. Growth occurs at the free end of each branch, where new cells are formed by the repeated division of a single *apical cell.*

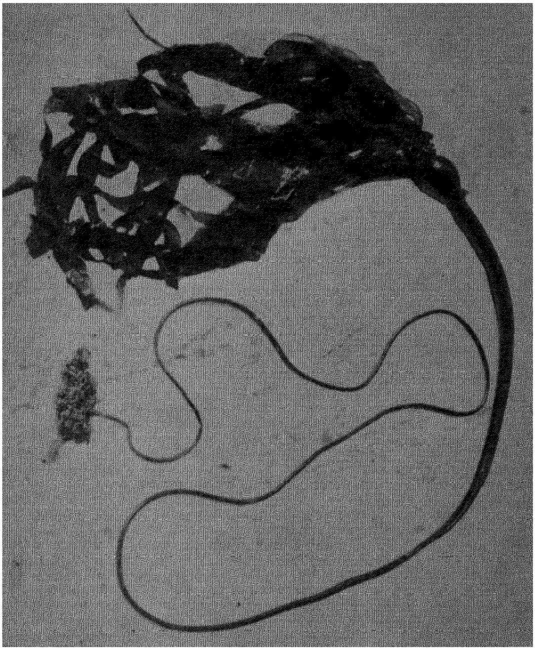


FIG. 172. Nereocystis, a giant kelp. Photograph by Lewis Josselyn.

175. Gametic Union. The free ends of the branches are often somewhat swollen, and in the swollen portions are numerous approximately spherical cavities each with a pore-like opening at its apex. It is in these cavities that the sex organs (oögonia and antheridia) are produced. In some species of Fucus, oögonia and antheridia are borne in the same cavity; in other species, the two kinds of organs are produced in separate cavities; in still other species, they are borne on separate plants. The cavities in which

antheridia are produced (Fig. 174, *B*) are lined with numerous branching many-celled hairs, the terminal cells of whose lateral branches become antheridia. The protoplast of each young antheridium divides, forming ultimately 64 small pear-shaped antherozoids each of which bears two unequal lateral flagella. The whole antheridium may be liberated and may ooze out through the pore of the cavity into the surrounding water, where its wall dissolves and the antherozoids become free. Sometimes the antherozoids are freed from the antheridium while the latter is still in place on the branch that produced it.

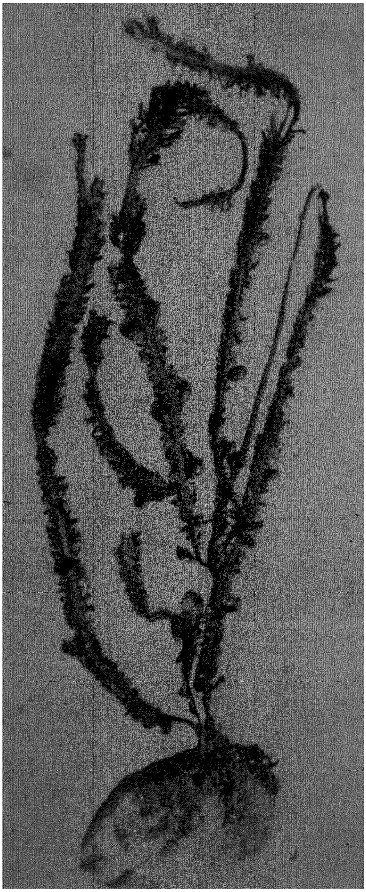


FIG. 173. Egregia, the "feather-boa" kelp, attached to a large stone by its holdfasts. Photograph by Lewis Josselyn.

The oögonia (Fig. 175, *A*, *B*) are borne at the ends of short stalks. The protoplast of each oögonium divides to form eight large eggs. When the oögonia are mature they break away from their stalks and float through the pore of the cavity into the surrounding water. Here the eggs are liberated by the rupture and dissolution of the oögonial wall. The eggs, being non-flagellate and therefore non-motile, become spherical when they are freed. Antherozoids that come into the neighborhood of an egg swim toward it, apparently in consequence of a chemical stimulus, and numerous antherozoids become attached by their flagella to the egg (Fig. 175, *C*). Eventually one antherozoid makes its way into the egg, the cytoplasm of the egg and that of the antherozoid unite, and their nuclei unite.

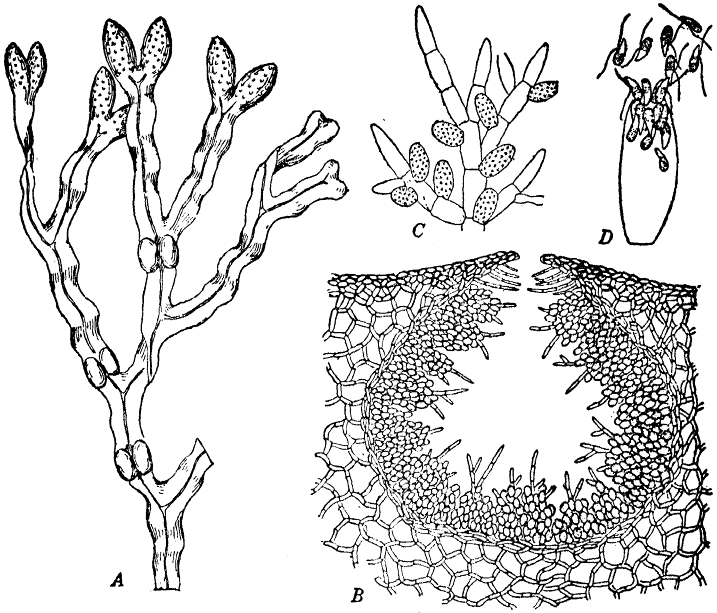


FIG. 174. Fucus. *A*, portion of a thallus, showing gas-containing vesicles and branches with swollen ends. *B*, cross section of a cavity containing antheridia. *C*, antheridial branch. *D*, antheridium at the time of the liberation of antherozoids. *B–D* redrawn from Thuret.

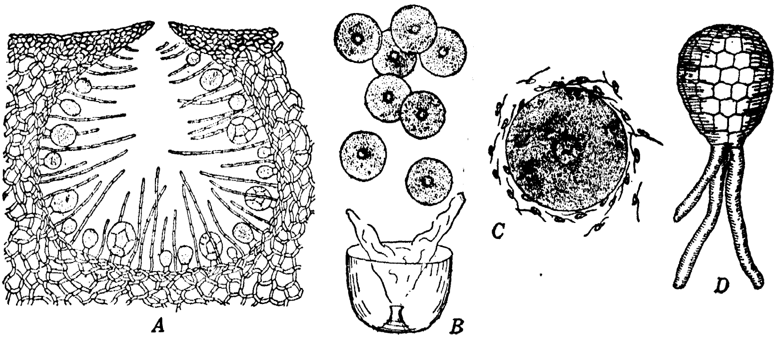


FIG. 175. Fucus. *A*, cross section of a cavity containing oögonia. *B*, oögonium that has burst and liberated eggs. *C*, gametic union. *D*, young plant produced by the germination of a zygote. All redrawn from Thuret.

After this union the zygote secretes a wall, and when it settles to the bottom of the water and comes into contact with some solid substance it develops into a new plant (Fig. 175, *D*). Under certain conditions an egg can develop into a new plant without uniting with an antherozoid.

FIG. 176. Portion of a thallus of the gulf weed, Sargassum.

176. Sargassum. Among other brown algae which, like Fucus, form small motile antherozoids and large non-motile eggs is the gulf weed (*Sargassum*, Fig. 176). It has essentially the same type of flat, branching thallus as Fucus, but commonly with more marked differentiation between stem-like and leaf-like branches. Having more numerous gas bladders than Fucus, it floats freely when detached from the substrate. Floating plants of Sargassum are particularly abundant in the warm waters of the Gulf Stream, and the presence of masses of these plants in the Atlantic gave rise to the fable of the "Sargasso Sea." Whether the floating plants have become detached, or are able to perpetuate themselves indefinitely in the floating condition, is still uncertain.

DIATOMS

177. Nature and Distribution. On the basis of the color of their plastids the diatoms seem to be distantly related to the brown algae, but they are considered as constituting a distinct class.

Diatoms occur in both fresh and salt water. They compose an important part of the plankton of the ocean, and in early spring and late fall make up the major portion of the plankton of fresh-water lakes. Other diatoms of both fresh and salt water grow intermingled with, and attached to, algae of other classes, or upon rocks and other solid bodies in the water.

The siliceous wall of a diatom does not decay after the death of

the cell, and great numbers of the walls accumulate at the bottom of any body of water in which diatoms live. Layers of fossil diatom walls deposited in former arms of the ocean are known as "diatomaceous earth." Some deposits of this nature in the western part of the United States are over 1,000 feet in thickness. Diatomaceous earth is of considerable economic importance as a heat-insulating material; it is also a source of fine abrasive substances. The abrasive qualities of some silver polishes and tooth pastes are due to fossil diatom walls.

178. Structure. Diatoms are usually unicellular; but in some species the cells are united into filamentous or branching colonies. The shape of the cell differs greatly in various species, but in all cases the wall consists of two overlapping halves that fit together as do the two parts of a candy box. The wall is strongly impregnated with silica. Cell walls of diatoms are characteristically marked by minute pores or short lines. The markings either are

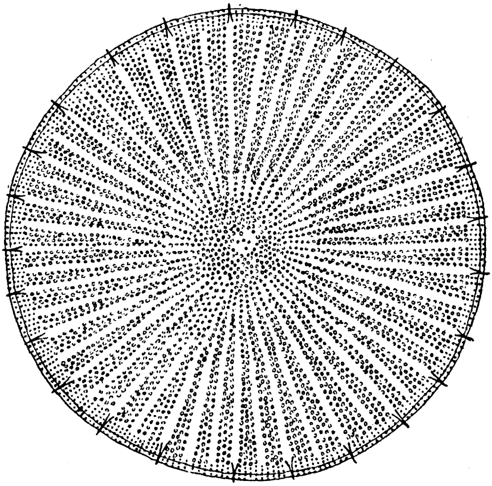


FIG. 177. A diatom (Stephanodiscus) with radial arrangement of cell-wall markings.

radially arranged with reference to a central point (Fig. 177); or their arrangement is bilaterally symmetrical with respect to the long axis of the cell (Fig. 178). There is a layer of dense cytoplasm just within the wall; within this layer is a central vacuole. Included in the dense cytoplasm are one, two, or several golden-brown plastids. The single nucleus is imbedded either in the outer dense cyto-

plasmic layer or in a strand of dense cytoplasm that cuts across the central vacuole.

179. Reproduction. Nuclear division is followed by a division of the whole protoplast, each of the two daughter protoplasts remaining within one of the closely fitting halves of the parent-cell wall. The development of a new half-wall over the naked face of each daughter protoplast completes the enclosure of the daughter cell by a typical two-parted wall. The daughter cells in most species separate; but in some species they remain attached. Of the daughter cells formed by division, one is of the same size as the parent cell, the other slightly smaller. In consequence of a continuation of reproduction by cell division, most of the cells in time are appreciably smaller than the original parent cell. The progressive diminution in size does not continue indefinitely, since a small cell may undergo changes in form and condition in the course of which it grows to the size of the original parent cell. In some cases such a rejuvenescent stage involves a rounding up of the protoplast within the siliceous half-walls. In other cases the rejuvenescent stage is a zygote formed by the union of two protoplasts.

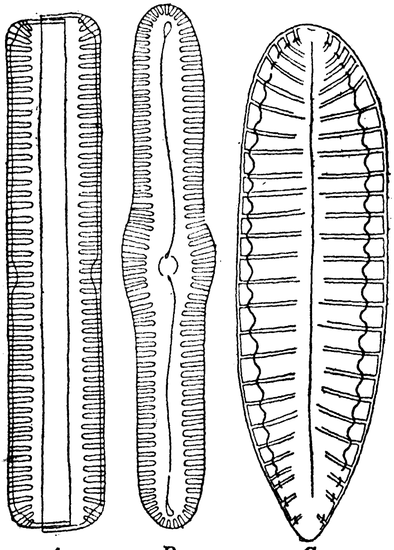


Fig. 178. Diatoms with bilaterally symmetrical arrangement of markings. *A*, *B*, top and side views of a Pinnularia. *C*, Surirella.

CHAPTER XVII

RHODOPHYCEAE (RED ALGAE)

180. Nature. The characteristic color of red algae is due to the presence of a pigment in the plastids, which masks the chlorophyll. Color, however, is not a certain criterion, since the thalli of certain species of this class are olive-green, golden-brown, deep olive-black, or purplish black. Among the structural features which distinguish red algae are the occurrence of non-flagellate male as well as female gametes and, in most species, the presence of broad cytoplasmic connections between adjoining cells of the thallus.

The union of non-motile gametes of different sizes characteristic of the red algae is so unlike gametic unions in other algae that the present group appears to have arisen entirely independently. Primitive one-celled organisms from which the red algae may have been derived are, however, unknown, and the origin of the class is obscure.

181. Distribution and Structure. Red, like brown algae, are almost exclusively marine. They are most abundant in the warmer waters of the oceans, although by no means absent in cooler regions. Red algae always grow attached to some solid object, and usually below the levels exposed by tides. In cooler waters the lowest depths at which algae, chiefly reds, occur are 150 to 180 feet, but in regions somewhat nearer the equator, such as the Mediterranean, where a larger proportion of the days are sunny and where the sun's rays penetrate the water directly during a greater part of the year, red algae have been dredged from depths of 300 to 600 feet. A few red algae, including members of the widespread genus *Batrachospermum*, live in fresh water.

Although no red algae attain to so great a size as do some brown algae, the numerous species of this class show much variation in both size and form (Fig. 179). In some, the thallus is a much-branched, feathery structure; in others it is flat and leaf-like, thin and delicate, or tough, leathery, and compact. The thalli of some red algae (Corallines) become incrusted with lime; these species

are of great importance in the formation of the "coral" reefs, atolls, and islands of tropical seas.

Of the two genera discussed in the following paragraphs, one is typical of those red algae whose structure and life cycle are

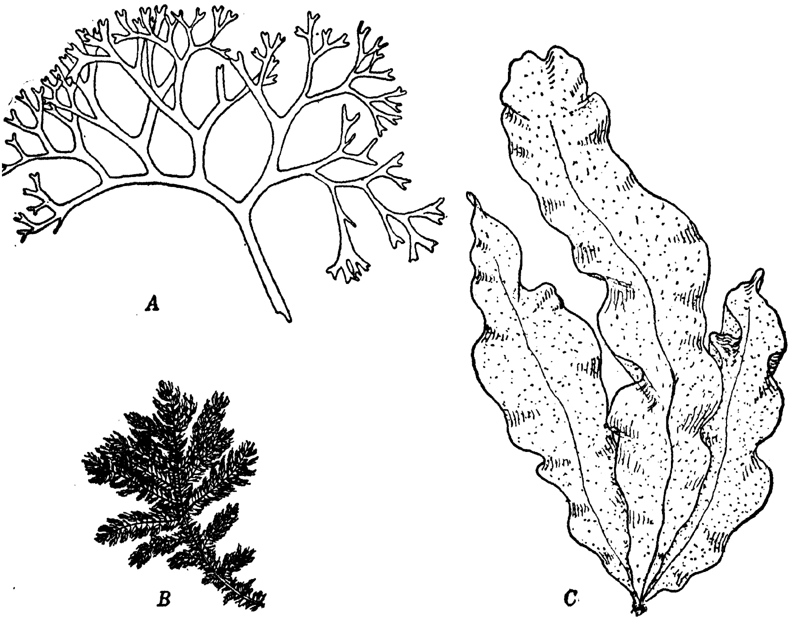


FIG. 179. Types of thalli found among red algae. *A*, thick branching thallus of Chondrus. *B*, feathery thallus of Polysiphonia. *C*, thin, leaf-like thallus of Grinnellia.

relatively simple; the other is representative of those with a more elaborate organization and a more complicated life cycle.

NEMALION

182. Structure. The plant (Fig. 180, *A*) is a long, slender, sparingly branched cylinder made up of a rather dense mass of interwoven, much-branched filaments imbedded in a gelatinous matrix. The central portion of the thallus consists chiefly of filaments which run lengthwise; numerous lateral branches, lying mostly at right angles to the central mass, form the dense outer portion. Adjacent cells within each filament are not completely separated by walls; there is a central pore of varying size in each

cross wall through which the protoplasts are in contact. The cells are one-nucleate, and each cell in the outer portion of the thallus contains a single star-shaped plastid, within which is a pyrenoid surrounded by starch granules.

183. Gametic Union. Male gametes (*spermatia*) are produced in dense clusters at the ends of short branches (Fig. 180, *B*). Each

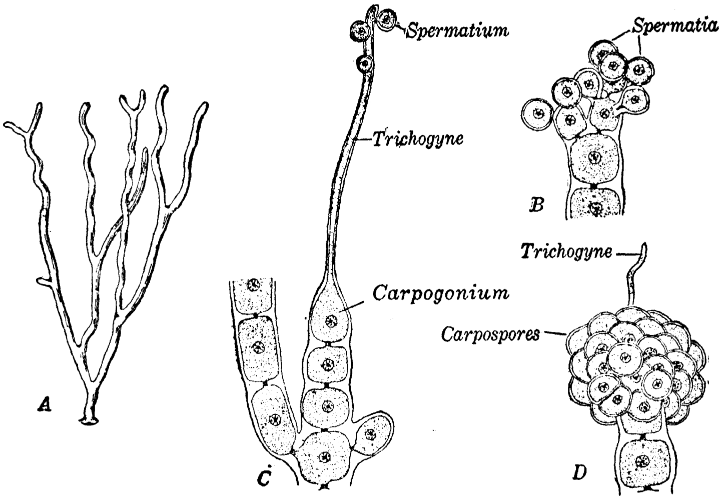


FIG. 180. Nemalion. *A*, thallus. *B*, portion of a branch bearing spermatia. *C*, portion of a branch bearing a carpogonium. *D*, cluster of carpospores borne on branches that have grown from the zygote.

spermatium is a small, non-motile cell. The spermatia become dislodged and are carried in all directions by water currents.

A female organ (*carpogonium*) is the terminal cell of a short lateral branch (Fig. 180, *C*). The free end of the carpogonium is prolonged into a long hair-like outgrowth, the *trichogyne*. The basal portion of the protoplast of the carpogonium, including its nucleus, is the egg. Spermatia carried by water currents may lodge against the trichogyne. When spermatia come into contact with the trichogyne they adhere to it; the walls of one spermatium and of the trichogyne break down at the point of contact, and the protoplast of the spermatium moves into the trichogyne. Shortly after entering the trichogyne, the nucleus of the spermatium divides; the two male nuclei so formed move toward the base of the carpogonium, and one of them, reaching the enlarged basal por-

tion, unites with the egg nucleus. After this nuclear union, numerous short branches develop from the zygote, the terminal cell of each branch becoming a *carpospore.* The carpospores, which are borne in a dense cluster (Fig. 180, *D*), eventually become separated from the branches, float away, and develop into new plants.

Polysiphonia

184. Structure. The feathery thallus of *Polysiphonia* (Fig. 181, *A*) consists of a much-divided system of relatively large branches which bear many smaller branches. Each of the larger branches consists of several superimposed tiers of cells which are elongated in the direction of the length of the branch. Each tier consists of a central cell and a surrounding jacket layer one cell in thickness. At each end of the central cell is a thick cytoplasmic strand connecting it with the central cell of the adjoining tier. The jacket cells of each tier are similarly connected with the central cell of the same tier. Each of the smaller branches of the thallus consists of but one row of cells, connected by cytoplasmic strands. All cells are one-nucleate, and each contains many small disk-shaped plastids.

185. Gametic Union. Male and female gametes are borne on separate plants. The spermatia are densely crowded on club-shaped lateral branches (Fig. 181, *B*). When mature, the spermatia become separated from the branches bearing them and are transported by water currents.

A carpogonium (Fig. 182, *A*) is the terminal member of a short lateral branch of five cells. It is similar to a carpogonium of Nemalion, consisting of a hair-like terminal trichogyne and an enlarged basal portion.

As in Nemalion, spermatia carried by water currents may lodge against, and become attached to, a trichogyne. The walls between a spermatium and the trichogyne break down at the point of contact, and the protoplast of the spermatium migrates into the trichogyne. The spermatium nucleus moves down the trichogyne until it comes into contact with the nucleus of the egg. There is no division of the spermatium nucleus, as in Nemalion. The union of the gamete nuclei forms a zygote nucleus. The five-celled branch bearing the carpogonium has by this time produced additional cells, and the zygote nucleus migrates through one of these new cells into the basal cell of the branch, which now is very irregular

CHAPTER XIX

PHYCOMYCETES

203. Filamentous Fungi. There are many simple plants which, like bacteria, do not contain chlorophyll; all these plants are classed together as fungi. The bacteria are the simplest fungi. The great majority of fungi are more complex than bacteria in the fact that their bodies, whether one- or many-celled, are composed of branching filaments. One large class of (chiefly) filamentous fungi which, particularly in their methods of formation and union of gametes, are more or less like certain algae are known as *Phycomycetes* (algal fungi). In some phycomycetes there occurs a union of gametes that are nearly or quite alike in size and structure. Others are characterized by the union of very unlike gametes.

RHIZOPUS

204. Structure. Among phycomycetes with like gametes is included an order known as "black molds." One of these is the

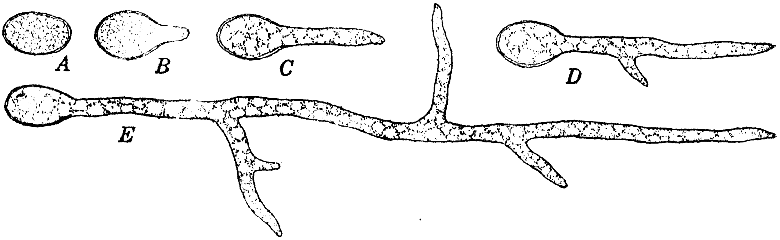


FIG. 193. Stages in the germination of a spore of Rhizopus and the development of a mycelium.

common bread mold (*Rhizopus nigricans*), which forms an abundant soft, white, cottony growth on moist bread. The plant body is a filamentous, much-branched structure, each branch (*hypha*) being a slender thread. The whole complex of hyphae is a *mycelium*.

The dark-colored spores produced by the bread mold are variable in size and shape, though usually ovoid (Fig. 193, *A*). When a spore comes in contact with water, it soon enlarges and becomes

spherical; its wall, formerly wrinkled, becomes smooth. These changes result from the fact that the protoplasm absorbs water, swells, and exerts pressure on the wall. A little later, if the temperature is favorable, the outer layer of the wall breaks (Fig. 193, *B–E*) and a short hypha, surrounded by the innermost layer of the wall, protrudes. This hypha elongates rapidly, branches, and so gives rise to a young mycelium. If a spore is sown in water, the mycelium growing from it soon dies because the only available food is the small amount present in the spore. On the other hand, if a spore germinates in a nutrient liquid or on a piece of moist bread or other similar source of foods, growth continues until a much-branched mycelium is formed.

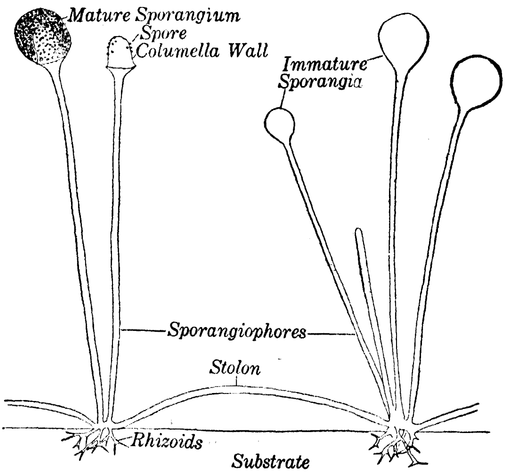


FIG. 194. Portion of a mycelium of Rhizopus.

A young hypha has a cell wall, within which is a granular cytoplasm; this contains many vacuoles of varying sizes, droplets of oil, and glycogen (a carbohydrate similar to starch), and includes numerous small nuclei. The protoplasm is in continuous movement, chiefly toward the tips of the various branches. The entire mycelium is as yet but a single undivided cell. An older plant (Fig. 194) is composed of hyphae of three types. Hyphae of one sort (*rhizoids*) anchor the plant and penetrate the substrate. The rhizoids, and a few other hyphae that come into contact with the bread or other substrate, secrete enzymes which digest the foods there present. The digested foods are absorbed by the mycelium and used in its growth. Certain other hyphae (*stolons*), usually larger than the rhizoids, grow approximately parallel to and above the substrate for a distance and then, bending downward, each stolon develops another group of rhizoids. Hyphae of a third type grow upward from the stolons at points where the rhizoids are formed.

Each of these erect hyphae (*sporangiophores*) bears a *sporangium*.

205. Spore-formation. A young sporangiophore elongates considerably. Into its enlarging tip, now the sporangium, protoplasm migrates containing much food and many nuclei (Fig. 195). As this protoplasmic movement continues, the portion of the protoplasm containing most of the nuclei and food aggregates in the outer part of the enlarging sporangium, leaving the center occupied by protoplasm with many large vacuoles and few nuclei. Some of the vacuoles become arranged in a dome-shaped layer between the outer, denser and the inner, less dense protoplasm (Fig. 196, *A*). These vacuoles soon become flattened, and as they come into contact with one another they unite into larger vacuoles until finally their union

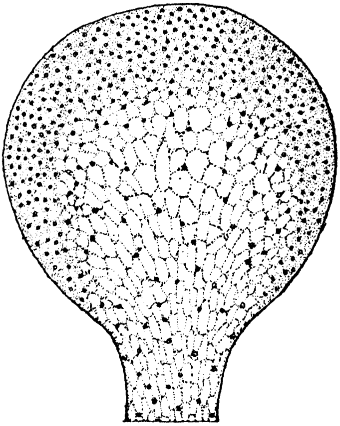


FIG. 195. Apex of a young sporangiophore of Rhizopus.

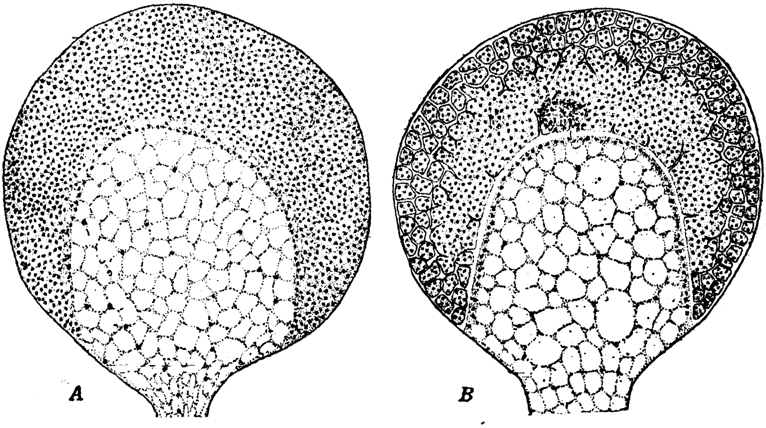


FIG. 196. Stages in the development of a sporangium of Rhizopus. *A*, just before the cell division separating the columella (inner part) from the spore sac proper. *B*, division of the protoplast of the spore sac into spores.

forms a cleft separating the outer from the inner part of the sporangium. The united vacuolar membranes form a plasma

membrane on each side of the cleft. The cleft is completed by a furrowing of the original plasma membrane about the base of the sporangium (Fig. 196, *B*). Between the two new plasma membranes a wall is secreted, which thus separates the dome-shaped central part of the sporangium (the *columella*) from the outer part, the spore sac proper. The latter is now a separate cell provided with a continuous plasma membrane. This membrane becomes furrowed in numerous places, both on the side next the outer wall and on that next the columella wall. The furrows cut into the protoplasm, branching, and dividing the contents of the spore sac into smaller and smaller protoplasts of irregular shape. The small cells ultimately produced by this process of *progressive cleavage* are the spores, each containing a variable number (2–10) of nuclei. This method of division by means of furrows which progressively divide a many-nucleate cell into smaller and smaller cells occurs also in some other fungi, as well as in a few algae. It is very different from division by means of a cell plate or by constriction.

Finally the newly formed spores become rounded and each secretes a wall. The outer wall of the spore sac dries and becomes fragile when the spores are mature, and any slight disturbance breaks it, liberating the spores. The columella persists as a dome-shaped structure at the end of the sporangiophore (Fig. 194). A mycelium usually remains one-celled until columella-formation takes place in the sporangia, but after this time cell division by constriction may occur and cross walls be formed in various portions of the mycelium. At any stage of development, however, under unfavorable environmental conditions, divisions may occur in the hyphae. Even after such divisions, each of the cells that constitute the plant, except the spores, is comparatively large and many-nucleate.

206. Formation and Union of Gametes (Fig. 197). Gametic union in Rhizopus resembles the corresponding process in Spirogyra in that the two gametes are alike in size and are without flagella. When two hyphae of separate Rhizopus plants of distinct strains (see next paragraph) come into contact, a short side branch (*progamete*) may be produced by each hypha at the point of contact. The terminal portion of each progamete becomes swollen. Within this swollen portion a transverse division occurs and a cross wall is secreted, the many-nucleate end cell so formed

being a gamete. The basal portion of each progamete, which connects the gamete with the mycelium, is the *suspensor.* In time the walls between the two gametes, where they are in contact, dissolve, and the gametes unite to form a zygote. The zygote wall becomes very thick and black, and has a rough outer surface.

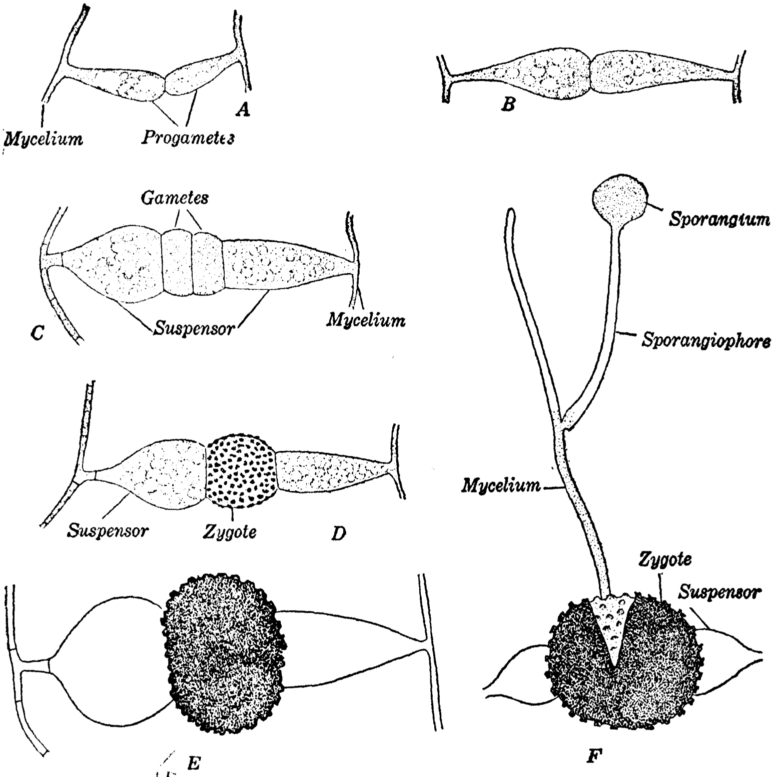


FIG. 197. Rhizopus. *A*, *B*, stages in the development of progametes. *C*, after the division of the progametes to form gametes and suspensors. *D*, *E*, young and mature zygotes. *F*, germination of a zygote.

The thick-walled resting zygote contains an abundance of reserve foods, largely in the form of fats, as well as many nuclei derived from each of the gametes. The subsequent history of the nuclei in the zygote is not fully known, but it is very probable that some of them at least unite in pairs. After a period of rest the zygote germinates (Fig. 197, *F*), giving rise to a hypha which soon forms a sporangiophore and a sporangium. This sporangium, except for

its smaller size, is similar to the sporangia produced on the ordinary mycelium.

The plants of Rhizopus belong to strains of two different sorts, referred to as *plus* and *minus*. No gametes are formed unless a hypha of a plus mycelium comes into contact with one of a minus mycelium. In Spirogyra, the two uniting gametes are conspicuously different in behavior, so that they may be designated as male and female. In Rhizopus the two gametes are often different in size; but such differences are too variable to make it certain that they represent a sexual differentiation. A few black molds, however, have distinctly different male and female gametes.

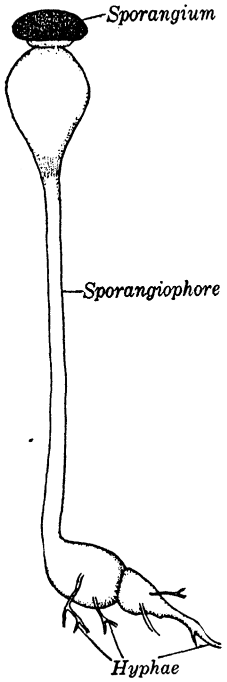


FIG. 198. Portion of the mycelium of Pilobolus, a black mold, with sporangiophore and sporangium.

207. Relatives of Rhizopus. While Rhizopus is the one most commonly found in the household, several other black molds are widespread. One of these (*Phycomyces*) has sporangiophores which often reach a height of several inches. *Pilobolus* (Figs. 198, 199), frequently found in barnyard refuse, has a mechanism for throwing the entire sporangium to a distance of more than six feet. Although the majority of black molds are saprophytic, a few are parasitic on other fungi, and some cause important diseases of both plants and animals.

Among other phycomycetes with like gametes, which are possibly related to the black molds, the best known are species of *Empusa*. One member of this genus is a parasite of the common house-fly and kills great numbers of flies. Its mycelium is composed of many short cells, each containing one to several conspicuous nuclei.

SAPROLEGNIA

208. Nature and Structure. *Saprolegnia* (Fig. 200) is one of the commonest of those phycomycetes that produce male and female gametes which differ greatly in size, structure, and behavior.

Its species and those of other members of the same order are commonly found in water, growing on the living or dead bodies of insects and fishes and often on other plant and animal substances. For this reason these fungi are called "water molds." However, many if not all of them are abundant in surface soils. Saprolegnia and its immediate relatives are usually saprophytic; but under some conditions they become parasitic upon fish, probably gaining

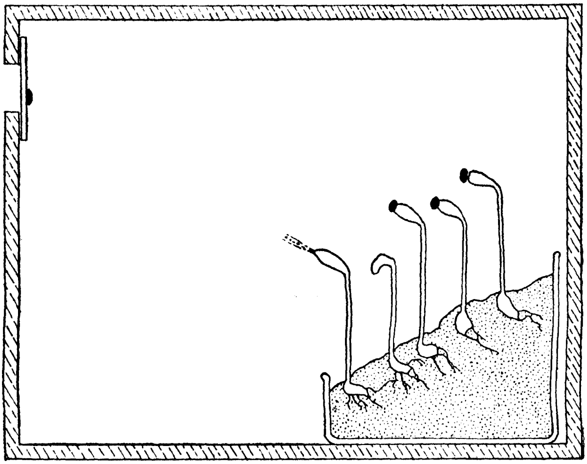


FIG. 199. A culture of Pilobolus placed in a dark box. The sporangiophores bend toward the small window through which light is admitted, and the sporangia are discharged toward the window.

entrance to the bodies of the hosts through wounds, and producing a destructive epidemic disease. Root diseases of many plants also are caused by fungi closely related to Saprolegnia.

The mycelium consists of hyphae, some of which are short and penetrate the substrate, while others are long and extend in all directions from the material upon which the fungus is growing. Like that of Rhizopus, the mycelium is, while young, a single much-branched, many-nucleate cell.

209. Spore-formation (Fig. 200, *A*, *B*). The protoplasm of the long external hyphae, at first vacuolate, gradually becomes denser and finally granular, especially at the tips. The tip of each hypha, becoming separated by cell division, forms a terminal many-nucleate sporangium. By means of furrows in the plasma membrane and of a flattening and branching of vacuoles, the protoplasm of the sporangium is divided into many small spherical

one-nucleate spores. The tip of the sporangium breaks, and through the opening so formed the spores emerge; each spore develops two flagella and finally swims away. After the swarm-spores have escaped, the basal wall of the sporangium becomes softened and is pushed up by the protoplasm below into the cavity

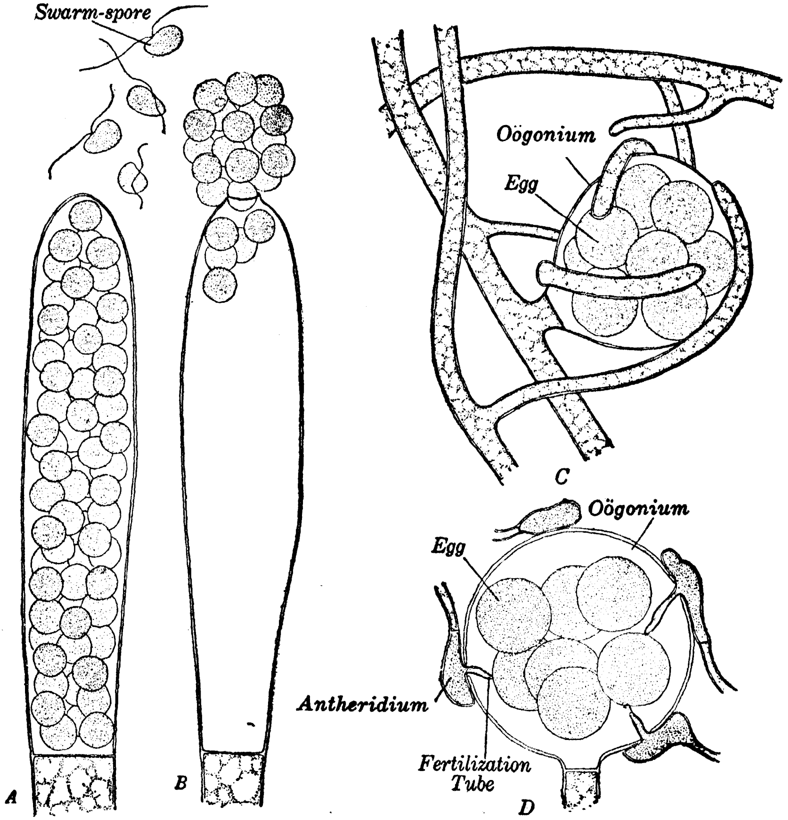


FIG. 200. Saprolegnia. *A*, sporangium containing spores. *B*, sporangium from which spores are emerging. *C*, oögonium surrounded by antheridial branches. *D*, after the formation of antheridia by the antheridial branches and the development of fertilization tubes.

of the old sporangium, where a new sporangium is formed. By a repetition of this process as many as three or four sporangia may be formed successively, each within the wall of the next older. A swarm-spore may swim about until it comes into contact with a source of food, when it comes to rest, withdraws its flagella,

secretes a cell wall, and develops into a slender hypha. This hypha penetrates the substrate, where it branches and develops into a mycelium.

210. Gametic Union (Fig. 200, *C*, *D*). Under some conditions certain hyphae produce sex organs instead of sporangia. The many-nucleate end of a hypha, cut off as a separate cell, develops in this case into an oögonium, which enlarges and becomes spherical. By a process of cleavage somewhat similar to that which occurs in a sporangium, the protoplasm of the oögonium is divided into a variable number (4–32) of female gametes (eggs).

Slender branches arising, some just beneath the oögonium, others on neighboring hyphae, grow toward, and become closely applied to, the oögonium. The slightly enlarged terminal portion of each of these hyphae is cut off as a many-nucleate antheridium. From the antheridium grows a slender *fertilization tube* which penetrates the oögonium and comes into contact with one or more eggs. In some species of Saprolegnia a nucleus and some cytoplasm, together constituting a small male gamete, pass from the antheridium through the fertilization tube into each egg. The zygote formed by union of the gametes secretes a thick wall. In other species, antheridia and fertilization tubes are not produced, or if produced do not function. Even in such cases, however, the eggs become thick-walled and have the appearance of zygotes. Under these conditions an egg functions as a spore, just as a gamete of Spirogyra sometimes does. The zygote or thick-walled spore usually enters upon a period of rest, and may retain its vitality for many months. The method of its germination is not well known.

The immediate relatives of Saprolegnia, members of the same order, resemble it in structure and in the general course of their life history. There are important differences between members of the order, however, in the structure of sporangia and in the methods of liberation and germination of swarm-spores.

Albugo

211. Nature and Structure. All species of *Albugo* are parasitic. A very common one infects the radish, cress, mustard, shepherd's purse, and related plants. The portions of the host plant containing the fungus, which may be leaves, stems, branches, flowers, or fruits, are often discolored or enlarged and markedly distorted

(Fig. 201). In time, white, mealy patches develop on the infected parts. Because of the appearance of these spots the disease is often called the "white rust." The mycelium of Albugo, like that of phycomycetes previously mentioned, is one-celled when young, many-nucleate, and composed of many hyphae which grow between the cells of the host. Foods are obtained by means of short, knob-like lateral branches that penetrate the walls of the host cells.

FIG. 201. Young radish plant infected by Albugo. The white spots are masses of spores.

212. Spore-formation. A time comes when, in consequence of a specially rapid branching of the mycelium, dense masses of hyphae are formed at various places beneath the epidermis of the host. Each hyphal mass gives rise to a layer of parallel stocky, thick-walled cells whose long axes are perpendicular to the epidermis (Fig. 202, *A*). Each cell of this layer elongates at its tip, and cell division cuts off a small, many-nucleate spore (*conidium;* Fig. 202, *B*). The cell below the spore elongates, and a second conidium is formed just beneath the first. By repetition of this process a chain of conidia is produced. The pressure caused by the elongation of numerous parallel spore chains finally breaks the epidermis of the host. It is the exposure of a mass of conidia that causes the mealy appearance characteristic of the fungus. The conidia are now easily detached from one another and scattered. When they germinate, each divides to form six or more two-flagellate swarm-spores which in turn can infect the host plant. The disease is spread throughout the growing season of the host by the production of successive crops of conidia.

213. Gametic Union (Fig. 203). After the formation of conidia, certain hyphae penetrate the deeper tissues of the host plant, especially those of the petioles or stem. In the intercellular spaces

of these tissues the tips of the hyphae enlarge, some becoming spherical and filled with a dense cytoplasm containing many nuclei. A cell division occurs which separates the enlarged tip

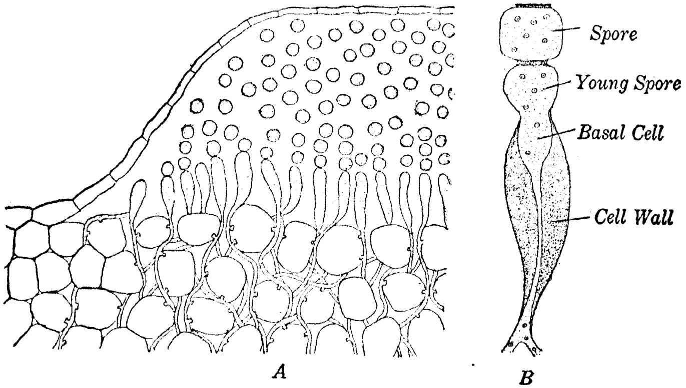


FIG. 202. Albugo. *A*, cross section of an infected radish leaf, showing the development of spores (conidia) beneath the epidermis (diagrammatic). *B*, enlarged view of the end of a hypha, showing the method of spore-formation.

(now an oögonium) from the rest of the hypha. Another cell division within the oögonium in time separates a single, usually one-nucleate, central egg from the surrounding many-nucleate

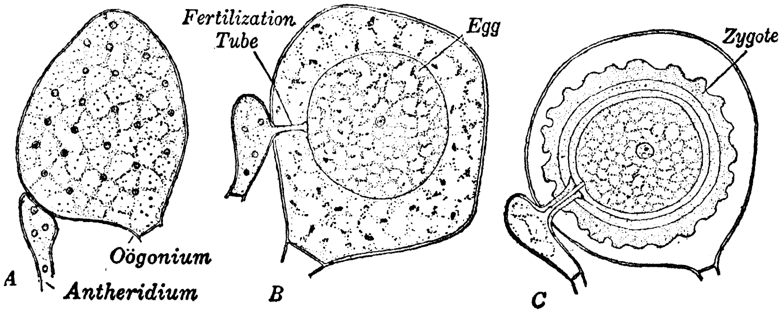


FIG. 203. Gametic union in Albugo. *A*, young oögonium and antheridium. *B*, oögonium in which an egg has been formed; the antheridium has developed a fertilization tube. *C*, old oögonium containing a zygote.

protoplasm. The egg is bounded by a plasma membrane, but no wall is formed between it and the peripheral cell. By this time the slightly enlarged tips of other hyphae have come into contact with the oögonium; the tips of these hyphae then by cell division become

antheridia. A slender fertilization tube from one antheridium pierces the wall of the oögonium and grows until it reaches the egg. A male gamete passes from the antheridium through the fertilization tube, enters the egg, and the male and female nuclei unite. The zygote formed by this union becomes surrounded by a thick wall. The cytoplasm and nuclei of the peripheral cell gradually disintegrate. Repeated nuclear divisions occur in the zygote, which at maturity contains typically 32 nuclei. After several weeks' rest the zygote may germinate. In germination, water is absorbed and cell and nuclear divisions occur, so that finally more than 100 two-flagellate, one-nucleate swarm-spores escape, each capable of infecting the host.

214. Relatives of Albugo. The "damping-off" fungus (*Pythium*), which causes wilting and decay in seed beds of various cultivated

FIG. 204. Early and late stages in the late blight of potato, caused by Phytophthora. Photograph by I. E. Melhus.

plants, the "downy mildew" (*Plasmopara*), which causes great losses to the grape industry in the United States and Europe, and *Phytophthora*, which causes the destructive "late blight" of the potato (Fig. 204), are all closely related to Albugo, differing from it mainly in the manner of production of their spores.

215. Relationships of Phycomycetes. The members of this class show considerable resemblances to certain algae. Rhizopus and

the other black molds are thought by some to have arisen from algae more or less like Spirogyra, because of the presence of similar or not greatly differentiated gametes and because of resemblances in methods of gamete-formation. The many-nucleate, undivided mycelium of the black molds renders this hypothesis questionable. It has been suggested, however, that there may be a connection through Empusa and some of its relatives, whose mycelia are made up largely or entirely of short cells each containing one large, centrally placed nucleus like that of Spirogyra.

Saprolegnia and its immediate relatives may have come from algal ancestors similar to Vaucheria. Vaucheria and Saprolegnia are alike in their undivided thalli with many small nuclei; in possessing motile spores; and in the differentiation between oögonium and antheridium, and between male and female gametes.

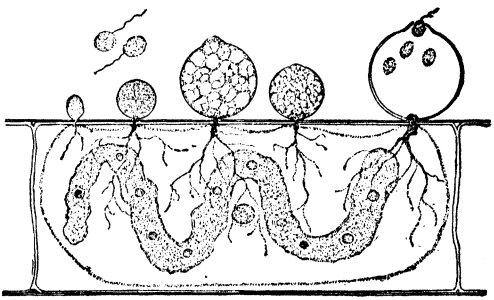


FIG. 205. Successive stages in the development of Rhizophidium, a chytrid parasitic upon Spirogyra. The Spirogyra cell shown is in very abnormal condition in consequence of infection by the parasite.

A large order of fungi (*Chytrids*), mostly aquatic and in large part parasitic, and very much simpler than either Rhizopus or Saprolegnia, should be mentioned here because they are usually listed with the phycomycetes. Some chytrids have naked many-nucleate protoplasts that give rise by progressive cleavage to spores. In other species the greater portion of the plant body is surrounded by a wall, but naked protoplasmic threads extend from this central portion into the host cell (Fig. 205). At maturity the walled portion functions as a sporangium. In still other species the entire protoplast is surrounded by a wall. Varying degrees of sexual differentiation between gametes appear among the chytrids.

Many chytrids give evidence of a not very remote relationship with flagellates. It is not unlikely, therefore, that included among the phycomycetes are forms descended from flagellates, as well as others, like Rhizopus and Saprolegnia, that have been derived from algae.

CHAPTER XX

ASCOMYCETES

216. Nature. Members of this, the largest class of fungi, vary greatly in form and structure. Some are saprophytic, some parasitic. All ascomycetes at some time in their history produce spore sacs (*asci*), within which are formed *ascospores*. The number of ascospores in an ascus is variable; in a large majority of species the number is eight. In addition to ascospores, various ascomycetes produce spores of one or more other types, some species having, including ascospores, as many as four spore forms.

YEASTS

217. Structure and Reproduction. A yeast is a fungus consisting of a single ovoid cell, or of a colony of two or more such cells. The most conspicuous feature of a yeast cell (Fig. 206, *A*) is a large

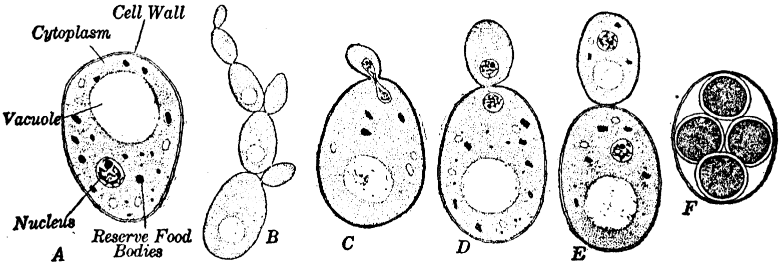


FIG. 206. Yeasts. *A*, mature yeast cell. *B*, colony formed by repeated cell division. *C–E*, stages in cell division. *F*, ascospores. *A*, *C–E*, from stained preparations. *B*, *F*, from living material.

vacuole lying in a finely granular dense cytoplasm. In the dense cytoplasm are also reserve food particles of varied shapes and sizes. Some of these are rounded masses of glycogen or globules of fat; others, more or less angular, consist of proteins. In specially stained cells it is possible to distinguish a nucleus with a chromatic network and a nucleolus. A cell wall which probably consists, in part at least, of chitin encloses the cell.

In a culture containing actively growing yeasts, cells of varying sizes are often united in colonies (Fig. 206, *B*). The cells composing

each colony have been derived from a single cell as a result of division and growth (Fig. 206, *C–E*). In the reproduction of a yeast under ordinary conditions, the nucleus divides in essentially the same manner as do the nuclei of more complex plants. A small localized area of the wall, usually at or near one end of the cell, becomes softened, probably as a result of enzymatic action. The wall bulges in the region of softening, a swelling or bud thus being produced. As this bud is forming, some of the cytoplasm and one daughter nucleus pass into it. A constriction of the plasma membrane in the plane of origin of the bud brings about a division of the cell into two daughter cells of very unequal size. The smaller of these daughter cells (the former bud) grows rapidly, and soon it also may produce a bud and divide in the same manner as the parent cell. The cells may remain attached or may separate.

Under conditions unfavorable for the ordinary development just described, such as a scarcity of food or water, a yeast cell often divides to produce a limited number, typically four, of one-nucleate cells which remain within the wall of the parent cell (Fig. 206, *F*). In this case the parent cell functions as a spore sac, (*ascus*), and the cells formed by division within the old cell wall are *ascospores*. With the return of conditions suitable for ordinary growth, the ascospores absorb water, grow, burst the wall of the spore sac, and develop into cells of the usual type. In many yeasts, including those of economic importance, no union of gametes occurs. The cells of a few yeasts, however, unite in pairs before forming ascospores, and thus function as gametes. This fact is considered by some investigators as evidence that the yeasts are descendants of ascomycetes that had a more complex life cycle.

218. Fermentation. It was known to the ancients that if a mixture of flour and water (dough) was allowed to stand, it would make a leavened bread very different from the unleavened bread baked immediately after the dough had been prepared, and that leavening would proceed more rapidly if sugar was added. It has long been a matter of general knowledge, too, that if fruit juices are exposed to the air and left undisturbed for a time, the liquid becomes cloudy, gases are given off, and, as the sugar disappears, the liquid becomes alcoholic. But not until European wine-makers and brewers became interested in an effort to control the flavors of wines and beers was something definite learned regarding the agencies concerned in the fermenting of fruit juices and in the

making of bread. Pasteur showed that these processes are due to the activities of yeasts and of other microörganisms.

Most yeasts can live and grow only in a solution containing a sugar, or substances that may readily be changed to sugars. Yeasts can not grow and multiply, however, unless other substances are present, because the carbon, hydrogen, and oxygen of a sugar are not the only elements necessary for the building up of living matter. If the solution containing the necessary food substances is in a thin layer, so permitting access to an abundant supply of air, the yeast cells will grow and divide rapidly, using a considerable portion of the sugar as a source of both building materials and energy. If, on the other hand, little oxygen is available, as when the yeast cells are so deeply immersed in the solution that most of them are cut off from the air, the majority of the cells settle to the bottom and there live as anaërobes. Under this condition the cells secrete an enzyme (*zymase*) which breaks down the sugar into alcohol and carbon dioxide, and the yeast makes use of some of the energy so released. Thus *alcoholic fermentation* is a type of respiration which, in the absence of free oxygen, replaces ordinary respiration as a source of energy for the yeast. A single species of yeast can apparently break down only a certain sugar or certain sugars, and

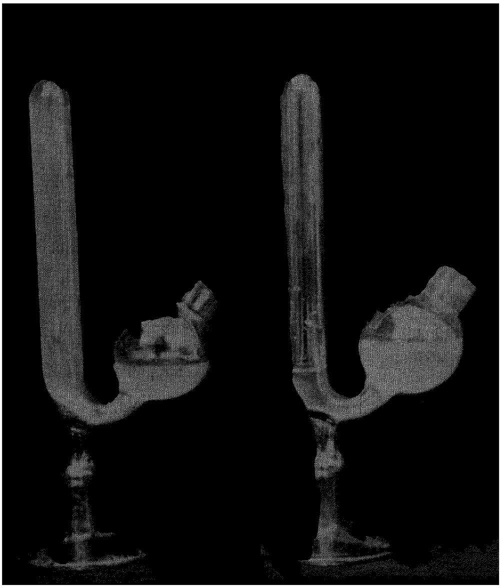


FIG. 207. Evolution of carbon dioxide during fermentation. The closed arm of the tube at the left is filled with a sugar solution containing yeast; the tube at the right shows the effect, after a few hours, of the production of carbon dioxide which has forced the liquid out of the closed arm.

some few rare yeasts are not known to cause alcoholic fermentation under any conditions.

The yeasts which bring about the fermentation of fruit juices in the making of wines and ciders are largely *wild* species. These yeasts live in or on the soil of vineyards and orchards and are carried with dust to the skins of the fruits. When the fruits are crushed, the yeasts are brought into contact with the fruit juices and fermentation ensues. The yeasts that ferment grape juice are of various species, and the characteristic flavors of different wines are due in large part to differences in the yeasts as well as in other organisms present, which cause, in addition to alcoholic fermentation, the formation of substances that modify the flavor of the wine.

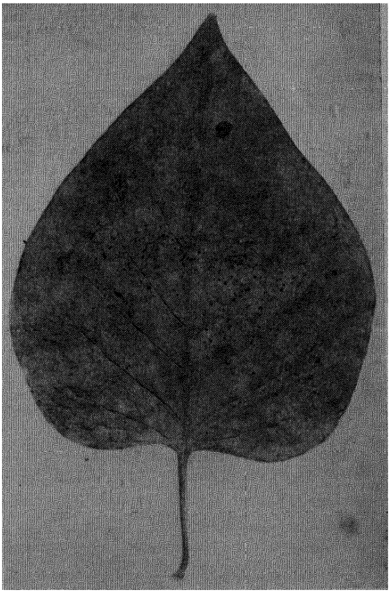


FIG. 208. Lilac leaf infected by a powdery mildew.

Yeasts used in brewing and in bread-making are *cultivated* yeasts. Cultures of these yeasts are grown and kept pure with the greatest care in order to prevent their contamination by wild yeasts and other organisms.

Some bacteria and several fungi other than yeasts are capable of inducing alcoholic fermentation. The production of alcohol by these organisms is encouraged by growing the bacteria and fungi under anaërobic conditions. A few black molds closely related to Rhizopus, as well as some species of Penicillium and Aspergillus (§ 221), readily form alcohol, and the commercial production of alcohol on a large scale is due in considerable measure to the activities of such fungi.

POWDERY MILDEWS

219. Structure and Reproduction. These parasitic fungi appear during the summer and fall, giving to the leaves or young stems of

their various host plants a whitish mealy or powdery appearance. The mycelium, composed of short one-nucleate cells, grows on the surface of a leaf or stem. Short branches from some of the cells of the mycelium, which act as absorbing organs, pierce the walls of

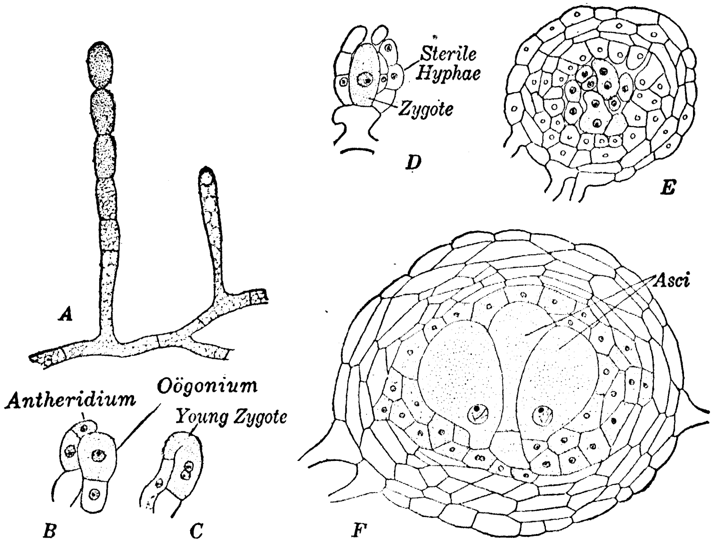


FIG. 209. Powdery mildews. *A*, Microsphaera; *B–D*, Sphaerotheca; *E*, *F*, Erysiphe. *A*, portion of a mycelium growing on the surface of a leaf and forming conidia at the end of a hypha. *B*, gametes. *C*, *D*, young zygotes. *E*, young fruiting body in which the cells derived from the zygote (shaded) are enclosed in a mass of cells from vegetative hyphae. *F*, cross section of a fruiting body at the time of the formation of asci. *B–F* redrawn from Harper.

the epidermal cells of the host, or, growing through stomata, penetrate the walls of the cells of underlying layers.

A common powdery mildew (*Microsphaera*) lives on the leaves of the lilac (Fig. 208). As soon as the mycelium has become well established on the host, some of its cells grow outward, perpendicularly to the surface of the leaf. The terminal portion of each of these elongated cells is separated by a cell division (Fig. 209, *A*) and becomes a short cylindrical spore (*conidium*). Other divisions occur successively below the first, so that a row of conidia is produced. The conidia are easily detached and separated from one another, and, since they can germinate immediately, are responsible for the rapid spread of the fungus to other leaves throughout the growing season.

220. Gametic Union. Sex organs are formed at the ends of special branches of the mycelium which grow so as to come into contact in pairs (Fig. 209, *B–D*). The slightly enlarged terminal cell of one branch of each pair is an antheridium; the much more enlarged terminal cell of the other branch is an oögonium. The one-nucleate protoplast of the oögonium functions as an egg; that of the antheridium as a male gamete. The walls at the point of contact between

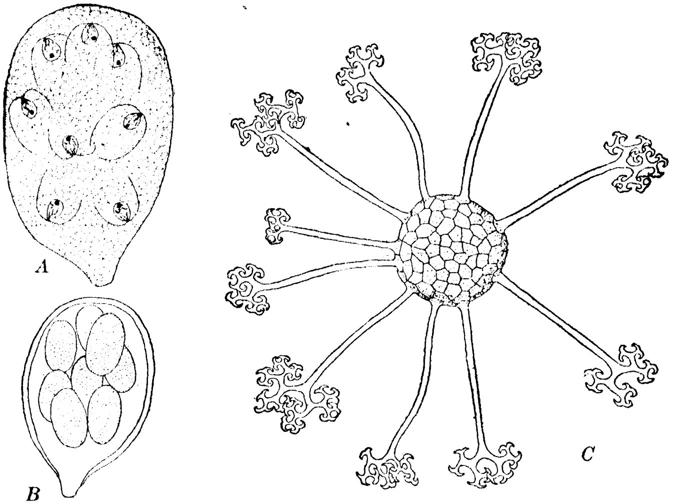


FIG. 210. Microsphaera. *A*, ascus forming ascospores. *B*, mature ascus. *C*, mature fruiting body.

oögonium and antheridium are dissolved, and through the opening so formed the male gamete passes into the oögonium. The nucleus of the male gamete and that of the egg unite, and the opening between antheridium and oögonium is later closed. The zygote formed by the union of egg and male gamete now divides, giving rise to a row of three to five cells. Branches arise from some of the cells of this row. Certain cells of these branches, containing two nuclei each, develop into asci. The two nuclei in each young ascus unite (Fig. 209, *F*), and, as soon as this nuclear union has taken place, the ascus begins to enlarge rapidly. During its enlargement the single nucleus now present divides, its daughter nuclei divide, and their daughter nuclei divide, so that the ascus contains eight nuclei distributed throughout its cytoplasm. By a process of cell division peculiar to the ascomycetes (*free-cell formation*), in which

not all the cytoplasm of the parent cell (the ascus) is included within the daughter cells, eight or fewer one-nucleate cells are formed inside the ascus (Fig. 210, *A*, *B*). These cells are ascospores.

After the union of egg and male gamete, the zygote becomes surrounded by hyphae which grow from the cells immediately beneath. While the asci are enlarging, the surrounding hyphae form a structure, black and almost spherical, in whose central portion the asci are enclosed (Fig. 210, *C*). Certain superficial cells of this fruiting body develop into greatly elongated appendages which (in Microsphaera) fork repeatedly toward their outer ends. The numerous fruiting bodies formed on an infected leaf become detached as the mycelium decays, and are scattered by winds. In the spring the outer layers of each fruiting body break down, exposing the asci, from which the ascospores escape. An ascospore falling on a lilac leaf may grow into a new mycelium.

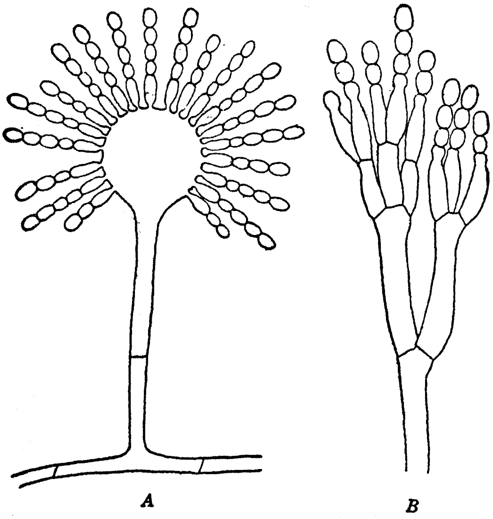
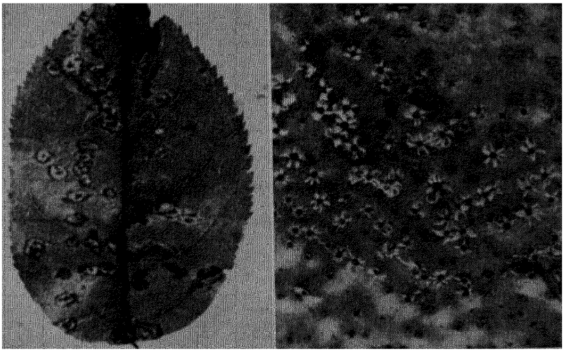


FIG. 211. *A*, lengthwise section of a conidium-bearing branch of Aspergillus. *B*, conidium-bearing branch of Penicillium. (Both figures diagrammatic.)

OTHER ASCOMYCETES

221. Blue and Green Molds. Certain ascomycetes form tangled mycelial masses on surfaces of decaying fruits, vegetables, and meats, as well as on damp leather and on a great variety of plant and animal substances. The characteristic flavor and mottled appearance of Roquefort and other cheeses are due to some of these fungi. Because of the general appearance of their mycelia, ascomycetes of this type are commonly spoken of as "molds." They differ from the black molds described in Chapter XIX in that their branching mycelium consists of relatively short one-nucleate cells, and also in their production of asci. Most of the ascomycetous

which appear to be the same as the rust upon the wheat and which are for convenience called by the same name (*Puccinia graminis*). But the uredospores of the stem rust of wheat will infect the oat only with difficulty and will not produce on the oat a serious disease. In the same way, uredospores from *Puccinia graminis* on oats, rye, or barley will not readily infect wheat. Both the rust on wheat and that on oats pass their aecidial stages upon the barberry. Such cases illustrate the fact that it is possible to differentiate races or species on the basis of their function (in this case of their ability to infect different hosts), although no distinction can be made on the basis of structure. Just as there are different strains of *Puccinia graminis* on wheat, oats, rye, and barley, so there are



A *B*

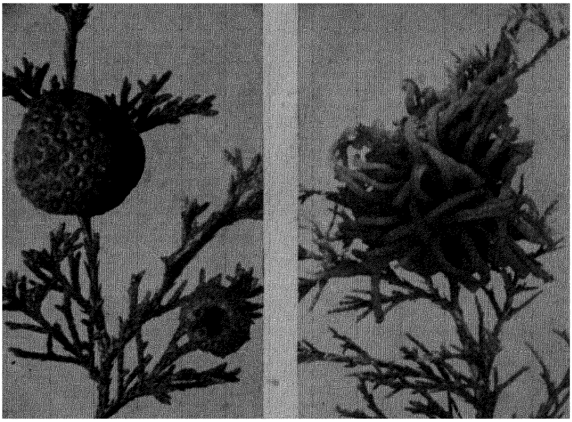
FIG. 225. Apple rust. *A*, apple leaf, showing groups of aecidia on its lower surface. *B*, enlarged view of an area bearing aecidia.

many distinct physiological races of this fungus each of which is limited to particular varieties of wheat. Similar conditions exist in other cereal rusts.

234. Other Rusts. The apple rust forms spermatia and aecidiospores on leaves and fruits of the apple (Fig. 225) and of some of its relatives. On the red cedar it produces swellings of the branches (so-called "cedar apples," Fig. 226) in which teleutospores are formed. A teleutospore, still attached to the host, germinates, producing a basidium and basidiospores. The basidiospores infect the apple. This rust forms no uredospores.

Some rusts, differently from the wheat and apple rusts, complete their life cycles on a single host. Examples of this sort are the rose

rust, the asparagus rust, the hollyhock rust, and the orange leaf rust of blackberries and raspberries. Many rusts have a shorter life cycle than the wheat rust. For example, the apple rust just mentioned produces no uredospores. The hollyhock rust represents the shortest known type of life cycle among the rusts; it produces only teleutospores and basidiospores. Although various rusts omit the formation of aecidiospores, spermatia, or uredospores, no rust



A *B*

FIG. 226. Apple rust. *A*, "cedar apples" on the red cedar. *B*, a cedar apple producing horn-like gelatinous projections on which teleutospores are formed.

is known which does not produce both teleutospores and basidiospores.

OTHER BASIDIOMYCETES

235. Field Mushroom. Numerous basidiomycetes, including many of the most conspicuous ones, are saprophytic. One of the commonest saprophytic basidiomycetes is the field mushroom (*Psalliota campestris*), which often grows in the rich soils of fields and open woods. This is the one mushroom that is extensively cultivated. Its vegetative body consists of colorless or whitish branching, short-celled hyphae which live for the most part underground. The cells of this mycelium are at first one-nucleate; but after a certain stage two-nucleate cells are formed, probably in consequence of a union of one-nucleate cells which therefore function as gametes. Some of the hyphae are interwoven into thicker

strands, but these strands, as well as the separate hyphae, are easily broken when the soil is disturbed. After the mycelium has

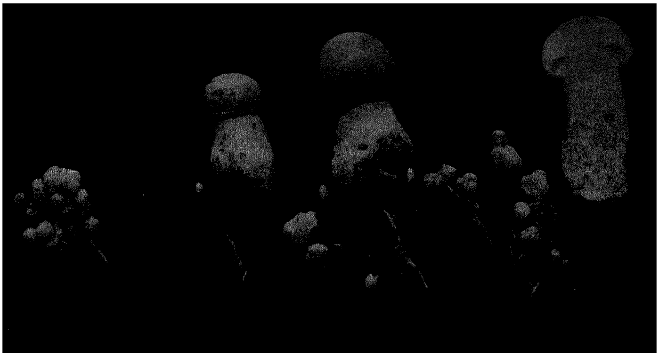


FIG. 227. Young fruiting bodies of the field mushroom (Psalliota) arising from the mycelium.

been developing for some time, compact, rounded masses of interwoven hyphae appear here and there on the underground strands. At first such a mass is almost microscopic; as it matures, it develops into the fruiting body commonly called a "mushroom" (Fig. 227). This body becomes differentiated into a stalk and a cap. The margin of the cap is attached to the stalk by a thin membrane which is broken as the cap enlarges. A portion of the membrane remains attached to the stalk in the form of a ring. Before the breaking of the membrane, the lower portion of the cap, extending from the stalk to the outer edge, has become transformed into many thin plates (*gills*), each free at its lower edge but attached above to the more compact portion of the cap. As the cap grows, it becomes much flattened so that the gills are fully exposed.

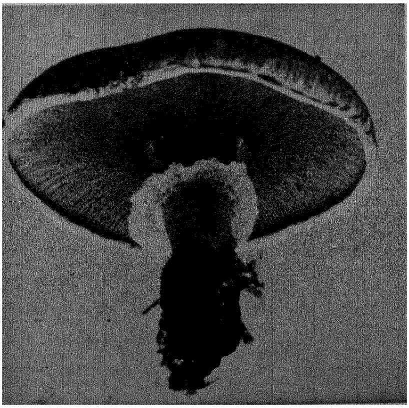


FIG. 228. Mature fruiting body of the field mushroom. Photograph by B. M. Duggar.

The mature cap (Fig. 228) is two to five inches in diameter; its top is white, cream-colored, or brownish; it bears many fine, silky hairs, and often some brownish scales. The flesh is white, turning to pink if broken. The gills are at first flesh-colored or pink, gradually changing, as the fruiting body grows older, to dark brown. The terminal cells of many of the hyphae which compose a gill

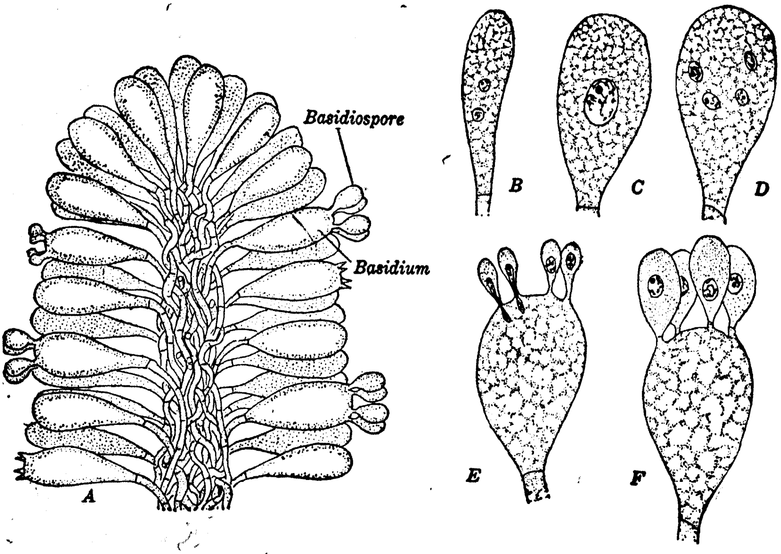


FIG. 229. *A*, diagram of a cross section of a portion of a gill of Psalliota. *B*, young 2-nucleate basidium. *C*, basidium after the union of the 2 nuclei. *D*, after the division of the zygote nucleus and of its daughter nuclei to form 4 nuclei. *E*, *F*, stages in spore-formation.

form a layer on each side of the gill (Fig. 229). The cells of this layer are parallel to one another and perpendicular to the surface of the gill. Most of the cells of the surface layer become much enlarged basidia. Each basidium is at first, like other cells of the mycelium, two-nucleate. The two nuclei in a basidium unite; this union is followed by two nuclear divisions, so that the basidium contains four nuclei. From the free end of each basidium grow two or four slender projections; the outer end of each projection swells, into it passes one of the nuclei of the basidium, and the enlarged end is cut off as a basidiospore. When a basidiospore germinates, it gives rise to a mycelium which may in time produce fruiting bodies.

236. Other Mushrooms. The "shaggy mane" (Fig. 230), which grows singly or in clusters on soil rich in humus, has a structure much like that of the field mushroom. The cap is long and narrow, and its upper surface bears numerous patches of hyphae interwoven in the form of strands and plates. As basidia and spores mature,

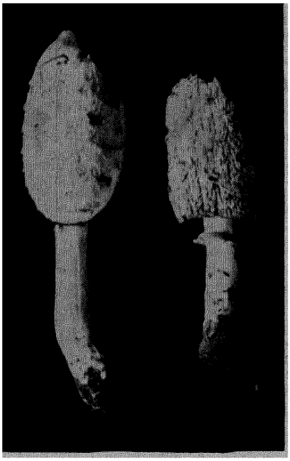


FIG. 230. The "shaggy mane," Coprinus.

FIG. 231. The deadly Amanita.

the cap darkens; its lower edge and eventually the whole cap softens and breaks down into black, slimy droplets. The shaggy mane and the closely related "inky cap" are edible.

Among the most beautiful as well as the most dangerous mushrooms are the deadly Amanita (Fig. 231) and the "fly mushroom," also an Amanita. At the base of the stalk of each of these mushrooms is a cup or bulb, from whose center arises the stalk with its conspicuous ring. The deadly Amanita has a pure white cap; that of the fly mushroom is reddish or orange-colored. Scattered over the upper surface of the fly mushroom are sometimes white wart-like elevations. The gills and the spores of both species are white.

The "honey mushroom" commonly occurs in clusters about

trees or stumps during late summer and autumn. Both stalk and cap are yellow or brownish. The stalk is tough and commonly bears a definite ring. Near the center of the cap are usually a number of erect dark scales. The "oyster mushroom" forms large clusters on trunks of dead or dying trees. The stalk is short and very thick and bears a large cap, often six inches in diameter. The stalk and cap are white. The name "oyster mushroom" was suggested by the shape of the cap, which is commonly much more developed on one side than on the other. Both the honey mushroom and the oyster mushroom are edible.

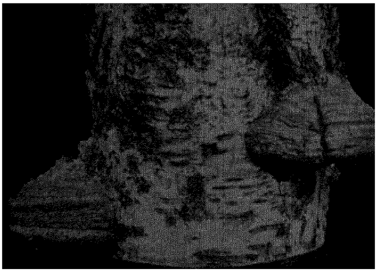


FIG. 232. Bracket fungi (Fomes) on the trunk of a birch.

There are no general rules for distinguishing between edible mushrooms and those which are unfit for food or poisonous. The one safe rule is to eat only mushrooms identified by an expert.

237. Bracket Fungi. Another considerable group of basidiomycetes live as saprophytes or parasites on various trees and shrubs. The mycelium penetrates the wood and on the external surface of the tree or shrub produces fruiting bodies of various forms. One of the simplest types of these fruiting bodies is composed merely of a crust-like layer of hyphae bearing basidia. Those of another type grow erect and are variously branched. In a third type, the branches of the fruiting body are covered with teeth or spines which project downward and whose outer surfaces bear basidia. The fruiting bodies of a fourth type are the so-called "brackets" (Fig. 232) that appear on stems and branches. Some of these brackets are soft, expanded outgrowths in whose lower

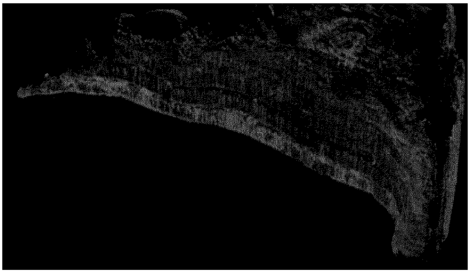


FIG. 233. Lengthwise section of a bracket fungus.

surfaces are innumerable fine pores lined with basidia. Most of such fleshy forms live for but a single season. The fruiting bodies of other bracket fungi are firm, hard, sometimes almost woody in texture, and grow in size from year to year, forming each year a

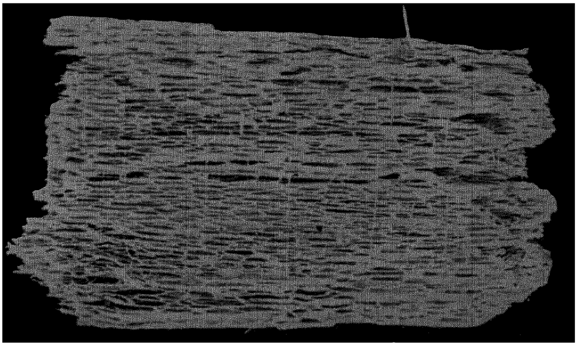


FIG. 234. Disintegration of wood caused by a bracket fungus.

new pore-containing layer below, and extending beyond, that of the previous year (Fig. 233). The fruiting bodies of *Fomes applanatus*, one of the commonest bracket fungi, are often 12 inches or more in diameter and may live for 10 years or longer.

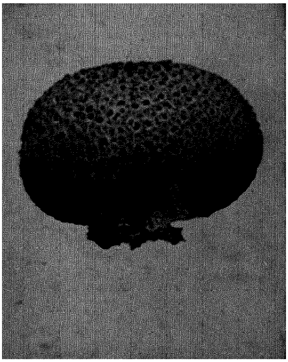


FIG. 235. A puffball.

The bracket fungi and their near relatives cause immense losses through the decay of the wood of living trees, as well as of logs and timber in lumber yards and of lumber in factories and warehouses. It is estimated that these "wood destroyers" cause each year more damage than forest fires.

238. Puffballs. The basidia and spores of another group of basidiomycetes are enclosed, often in special chambers, within the fruiting body. The spores of some species escape through special pores; those of others are set free only when the fruiting body decays or is accidentally broken. The best-known members of this group are the common "puffballs" of pastures and woods (Fig. 235).

The mycelium of a puffball grows in the soil or in rotting wood; on it are developed spherical bodies, comparable at first to an early stage of the field mushroom. These bodies grow, those of some of the giant puffballs reaching a diameter of 12 to 15 inches and a weight of several pounds. The interior of a puffball remains white until its full size is reached, when numerous scattered areas in the upper portion darken. This color change occurs at a time

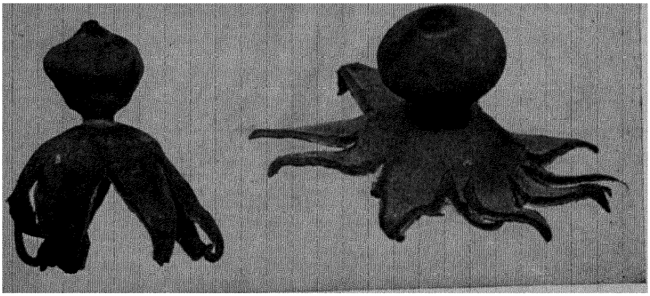


FIG. 236. The "earth star" (Geaster), a puffball.

when the ends of some hyphae have formed basidia. Other darkened areas appear successively within the fruiting body until finally the greater portion of its interior is filled with basidia and spores. Some of the hyphae surrounding the masses of spores disintegrate; other hyphae, whose walls become thickened, form a spongy network or serve as the boundaries of special chambers. The outer layer of the fruiting body in some species now opens by a definite pore, but in most puffballs it breaks irregularly or simply decays, and the spores escape.

239. Relationships. Smuts and rusts have not always been classed with the "true" basidiomycetes, such as the mushrooms. While these three groups are now usually treated as constituting a single class of which the smuts are most primitive, some writers still consider the smuts unrelated to the others.

As to the possible origin of basidiomycetes, little can be said. There is no group of algae from which they can readily be imagined to have been derived. The basidiospores have been likened to conidia, and some basidiomycetes produce true conidia that re-

semble those of some phycomycetes. The spermatia of rusts are similar to those of some ascomycetes. Basidiomycetes resemble ascomycetes also in possessing a mycelium composed at different stages of one- and two-nucleate cells. In other respects the mycelia are similar enough in the two classes to render plausible the conception of a relationship, perhaps through a remote common ancestry, between basidiomycetes and ascomycetes.

CHAPTER XXII

LICHENS

240. Nature and Forms. A lichen is peculiar in being formed by the intimate association of two very different plants, one of which is a filamentous fungus, the other in almost all instances an alga. The two organisms seem in most cases to derive mutual advantage from their association, the alga making carbohydrate foods

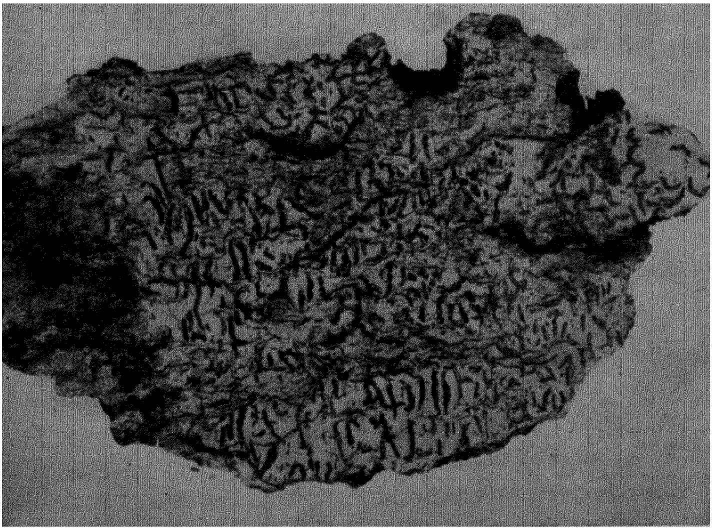


FIG. 237. A crustose lichen (*Graphis scripta*). The dark linear and curved structures are fruiting bodies.

and the fungus absorbing and retaining moisture for the partnership. In temperate regions, the fungal component is always an ascomycete; in a few lichens of warmer regions it is a basidiomycete. In the majority of lichens the other component is a one-celled green alga; in many, however, it is a blue-green alga. One lichen has been reported in which a filamentous fungus is associated with a bacterium rather than with an alga. The bacterium is of a species that

produces a red pigment. Lichens may be divided according to their forms into three principal types (Figs. 237–241): *crustose*, forming crusts on trees, rocks, or soil; *foliose*, with leaf-like thalli whose upper and lower surfaces are different; and *fruticose*, which are pendent or erect.

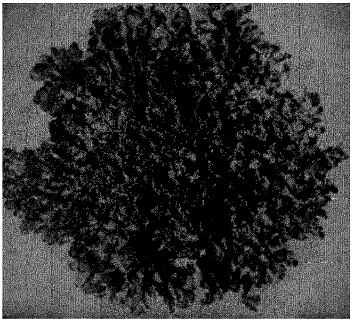


FIG. 238. Parmelia, a foliose lichen.

Crustose species vary greatly in form, color, and thickness. The body of such a lichen (Fig. 242, *A*) usually consists of an upper layer of closely packed and interwoven fungal hyphae, beneath this a layer of algal cells intermixed with hyphae, and finally a region of loosely woven hyphae which are intimately intermingled with the substrate. An additional lower closely packed layer is present in some species, especially in those which develop free lobes at the margin of the thallus. The bodies of some crustose lichens are partly or wholly imbedded in the bark, disintegrating rock, or soil upon which they grow. In the latter case, all that appears above the surface of the substrate may be the fruiting bodies of the lichen. *Graphis scripta* (Fig. 237) is a crustose lichen growing upon and partly imbedded within the smooth bark of some trees. Superficially it appears as an ashy or whitish crust on the surface of the bark, marked by black linear, curved, or branched fruiting bodies. Because of the resemblance of the fruiting bodies to hieroglyphic writing, this lichen has been observed and recorded since very ancient times.

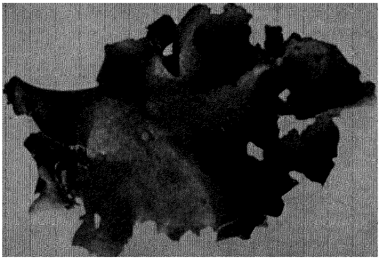


FIG. 239. Gyrophora, a foliose lichen.

A foliose lichen consists of one or more flat lobes which usually adhere more or less firmly to the substrate by means of strands of hyphae. The structure of the thallus is similar to that of a crustose lichen except that there is in all cases a well-developed lower closely packed layer from which grow holdfasts—strands of hyphae which

attach the thallus to the substrate. Some foliose lichens, such as *Gyrophora* (Fig. 239), are attached to the substrate each by a small central holdfast. On the lower sides of certain large foliose lichens are depressed, light-colored areas. In these areas the lowermost layer is lacking, and its absence allows a free passage of air to the algal layer.

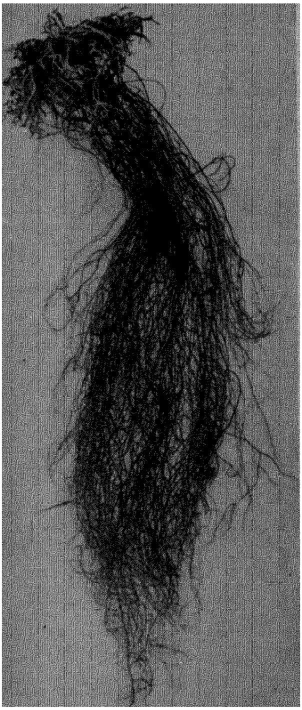


FIG. 240. "Old man's beard" (Usnea), a fruticose lichen.

The body of a fruticose lichen varies in shape from flat to cylindrical. Commonly it is much branched (Fig. 240). There is a central region of hyphae, surrounded by a zone containing algal cells, and this in turn by an outer zone of compact hyphae. There are no clearly differentiated upper and lower surfaces. The lichen is attached to the substrate by a definite basal portion composed of strands of densely packed hyphae. In some lichens, such as *Cladonia* (Fig. 244), the body is a combination of a crustose or foliose part with erect (fruticose) stalks.

241. Vegetative Multiplication. Any portion of the body of a lichen that is broken off may, under suitable conditions, develop independently. The commonest method of vegetative multiplication, and one found in most lichens, is by the development on the upper surface of minute bud-like outgrowths (*soredia*, Fig. 242, *B*). A soredium is composed of one or more algal cells surrounded by fungal hyphae. Soredia are formed at points at which the outermost layer of the thallus is interrupted, and are sometimes so abundant as to appear like dust on the surface of the thallus. Each soredium is pushed outward by the elongation of the hyphae to which it is attached; other soredia are formed below it, and later they too are pushed out. In certain species of lichens this is the only known method of reproduction of the thallus. Many lichens bear on their surfaces also

larger branching outgrowths, which likewise are composed of both fungal and algal elements. These outgrowths are easily broken off when dry, and under suitable conditions they may develop independently.

242. Spore-production. Minute dark pores appear on the surfaces of many lichens. Each such pore opens into a small cavity

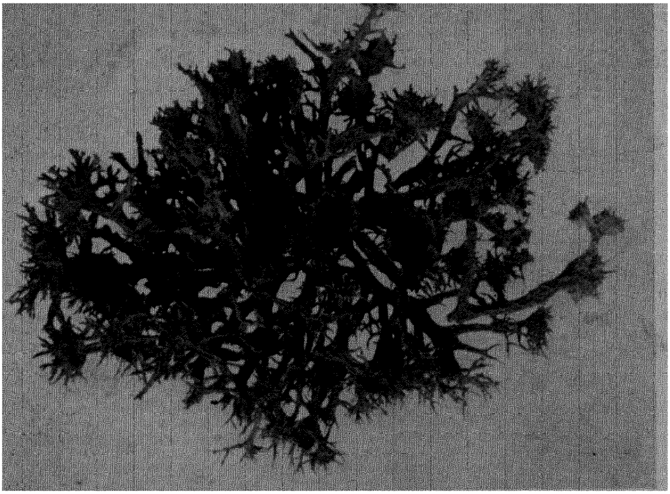


FIG. 241. A fruticose lichen (Evernia), with saucer-shaped fruiting bodies containing asci.

(*pycnidium*). At the tips of hyphae lining the cavity, spores (*pycnidiospores*) are formed. The spores are extruded and, if they germinate, produce new fungal hyphae. Experiments indicate that when these hyphae are grown in association with the appropriate algal cells, a lichen thallus results. In some lichens pycnidia are the only spore-forming organs known.

In case the fungal component is an ascomycete, asci are borne either in saucer-shaped (Fig. 243) or elongated (Fig. 237) structures on the surface of the lichen or in approximately spherical structures that are partly or entirely imbedded in the thallus. In a few lichens, the formation of asci has been shown to be preceded by a gametic union. Whatever the form of fruiting body, the included asci are intermingled with slender sterile hyphae (Fig. 242, *C*). Both asci and sterile hyphae grow approximately at right angles to the inner

surface of the fruiting body, constituting a fairly definite lining layer. Each ascus, in most lichens, contains eight ascospores. The spores are one-, two-, several-, or many-celled, their shapes varying with the genus and species.

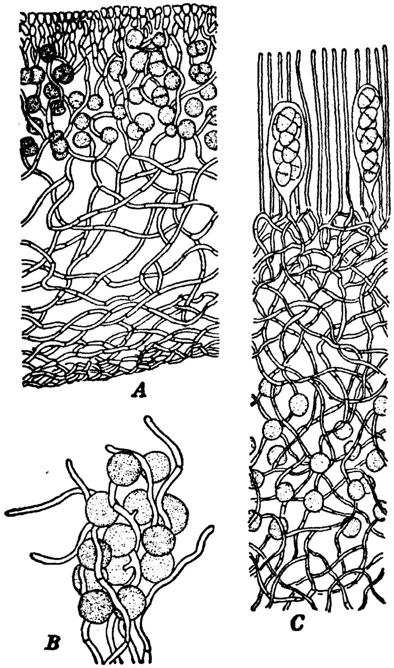


FIG. 242. *A*, cross section of the thallus of a lichen. *B*, a vegetative bud (soredium) which when broken away is capable of reproducing the thallus. *C*, cross section of a portion of a fruiting body, showing the formation of ascospores.

An ascospore, or each cell of an ascospore, may develop into a hypha which branches and elongates until its food supply is exhausted. If the hypha does not come into contact with algae of the species with which it is ordinarily associated, it dies; but if the appropriate algae are encountered, the fungus grows about the algal cells to form a lichen.

243. Practical Significance. Lichens play an important part in the formation of soil. Many crustose lichens gradually dissolve and disintegrate rocks to which they are attached. Lichens may be almost wholly imbedded in such rocks, the rock particles being held together by the gelatinized walls of the hyphae. When the lichens die they form, together with the disintegrated rock, a substrate for the growth of other lichens or for that of mosses, ferns, and seed plants.

The "reindeer moss" (*Cladonia rangiferina*, Fig. 244) is of considerable importance as a food for reindeer and cattle. It forms dense tufts sometimes twelve inches in height, and is abundant in extremely cold regions where other vegetation is practically nonexistent and where it may be buried in snow for long periods without injury. It grows equally well on sand, moist turf, or soils otherwise barren. "Iceland moss," another lichen, is similarly useful

in Iceland. The "rock tripe" of northern countries has been eaten by travelers when in danger of starvation. Another lichen (*Lec-*

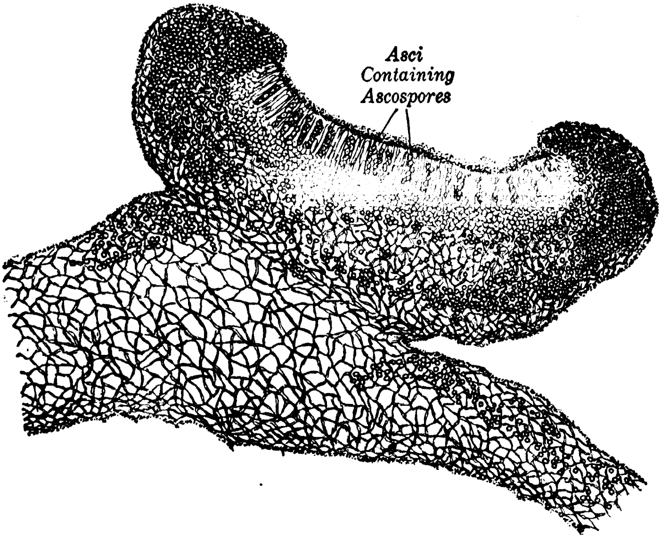


FIG. 243. Cross section of a fruiting body of a lichen.

anora esculenta) that has been used for food grows in the deserts of northern Africa. It is thought to have been the "manna" of

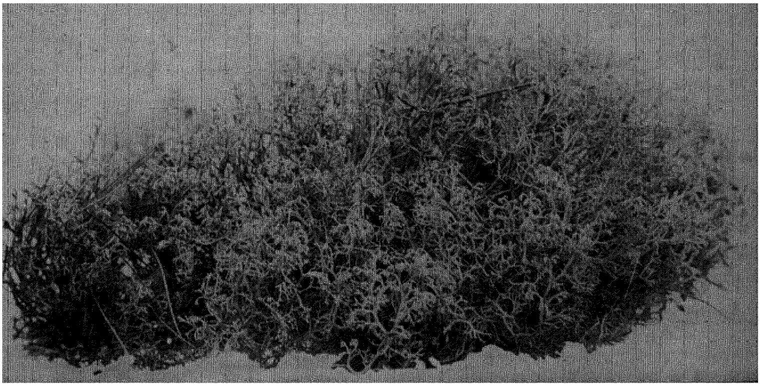


FIG. 244. The "reindeer moss" (*Cladonia rangiferina*).

the Israelites, and is still called the "bread of heaven." Many lichens were used by the ancients in the treatment of disease. The

"dog lichen" (*Peltigera canina*) was used as a cure for hydrophobia, and the "lungwort" (*Lobaria pulmonaria*) in the treatment of diseases of the lungs. The last-mentioned lichen has been used also in tanning, and as a substitute for hops in brewing.

The cell walls of the fungi in a number of lichens contain coloring substances. The most important of these coloring matters is orchil or cudbear, which is abundant in *Rocella tinctoria*. In extracting this pigment, the lichen is soaked in an alkaline solution until the latter attains a purple color. Orchil was formerly extensively used in the dyeing of woolen and silken fabrics.

CHAPTER XXIII

HEPATICAE (LIVERWORTS)

244. Nature. Liverworts are green plants, constituting one of the two classes of bryophytes. Their vegetative structure is in general more complex than that of any thallophyte. Most members of this class grow prostrate upon the surface of the substrate, although many of them produce branches or other organs that tend to grow upright. Some are strictly thallose; in others the plant body is differentiated into stem (and branches) and leaves, which organs, however, are almost or quite without distinction of tissues. Growth of the thallus or of a stem or branch is chiefly at one end—the anterior end or apex. Liverworts are sharply distinguished from thallophytes by the nature of their sex organs. These organs are always many-celled; some of their cells, at least those of the outermost layer, are sterile—that is, they do not develop into gametes.

The remote ancestors of this group must, it would seem, have been green algae; but whatever species of plants may have constituted links between algae and liverworts have long since disappeared. Most liverworts are terrestrial—that is, they live on soil, rocks, decaying wood, or the bark of trees. A few are aquatic (living in or on water), but these are clearly descended from terrestrial species. Since algae are characteristically aquatic, many of the features that distinguish liverworts from green algae are probably to be thought of as adaptations to a land habit. However, liverworts are still dependent upon an abundant supply of water, although some, such as certain species living on tree trunks, can withstand long periods of desiccation.

Riccia

245. Gametophyte. Members of the genus *Riccia* are among the simplest liverworts. Most of the 100 or more species of this genus live on moist soil, or rarely on rocks. Two of the most familiar species, however, *Riccia natans* and *Riccia fluitans*, often occur floating in pools, ponds, and lakes. In case the body of water

in which they are living partly or entirely disappears, the plants may be left upon the mud where they will continue to live and grow. A plant, especially one of *Riccia natans* (Fig. 245), growing on soil assumes a very different habit of growth from that which characterized it on the water. *Riccia natans* will be particularly described in the following paragraphs.

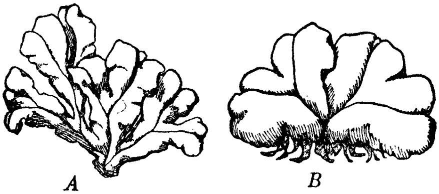


FIG. 245. Gametophytes of *Riccia natans*. *A*, a plant growing on land. *B*, a floating plant.

A spore of Riccia, under favorable conditions, germinates by swelling and pushing out at one side a filamentous outgrowth (Fig. 246). In this process, the outer layers of the spore wall are broken and the protruding filament is surrounded by an extension of the innermost layer of the wall. The dense cytoplasm and chloroplasts of the spore aggregate chiefly in the outer end of the filament; at this end, by a series of cell divisions, a small mass of cells is formed. By further growth and cell division this group of cells develops gradually into a mature plant.

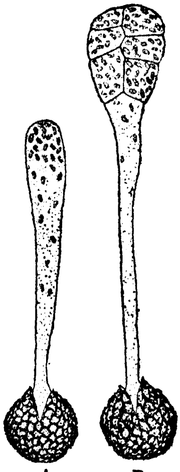


FIG. 246. *A*, germination of a spore of Riccia. *B*, early stage in the development of a thallus from a spore. Modified from Campbell.

The vegetative body is a thallus. When living on land, it is flat and at first approximately ribbon-shaped; it is thickest in the middle and gradually thinner toward the edges. The surface is more or less distinctly marked off into small rhomboidal areas. While still comparatively short the thallus forks at its growing end, producing two similar branches; in time each branch forks, and the process is indefinitely repeated. The result of this method of branching is the formation of a rosette-like plant. When it grows on water the thallus is thicker, and each branch grows but little in length before it in turn branches. The water form, consequently, has a more compact appearance than the land form. The apical portion of each branch can live through the winter and resume growth the following spring.

On the upper surface of a branch is a median longitudinal furrow.

This furrow is often less conspicuous, except at the apical end of the branch, in the water than in the land form. At the apex of the branch is a notch, and at the base of this notch a small group of embryonic cells. It is by the division of the cells of this group, and by the repeated division of those derived from them, that all the cells of the thallus are formed. The apices of the branches, therefore, are the regions of growth. Occasionally some cells in the center of an apical group of embryonic cells cease dividing. The apical group thus becomes separated into two groups of embryonic cells. In consequence of the formation of daughter cells which lie between these groups, the two embryonic regions gradually diverge, and ultimately the thallus forks, each fork or branch now having its own group of embryonic cells. In time the older parts of the thallus begin to undergo progressive death and decay. When decay reaches a point at which branching occurred, the surviving parts constitute two separate plants. Therefore, as a result of apical growth, branching, and the progressive death of older portions, the number of plants is from time to time increased. Adventitious buds are sometimes produced on the lower surface of the thallus which, if they become separated, may grow into new plants. It appears, too, that any cell or group of cells may, in response to an effective stimulus such as that supplied by a wound, develop an outgrowth that will become a new thallus.

In the apical region small intercellular spaces (air chambers) appear, which later extend to the surface of the thallus and increase in size with the growth and division of surrounding cells. The external openings of these chambers (Fig. 247) are narrow pores, each surrounded by a ring of five or six small cells. The air chambers become divided by partitions, each a single layer of cells; the interior chambers so formed are sometimes connected with one another and with those of the outermost layer by pores. In a mature part of the thallus, the greater proportion of its thickness is occupied by the numerous air chambers. The upper surface of the thallus is formed by a single layer of cells which bounds the outermost air chambers. The cells of the surface layer, as well as those constituting the partitions between chambers, contain many small chloroplasts; these cells, having access through air chambers and pores to the gases of the atmosphere, can carry on photosynthesis. The part of the thallus below the air chambers varies in thickness from one layer of cells at the margins to several layers

in the median portion; indeed, in the median region air chambers may be entirely lacking. The cells of this lower tissue contain few or no chloroplasts; some of the cells are filled with masses of oil mixed with other substances. From the lower surface of the thallus grow many long, narrow scales, each a single layer of cells. Some cells of the lower surface grow out into long, slender rhizoids which

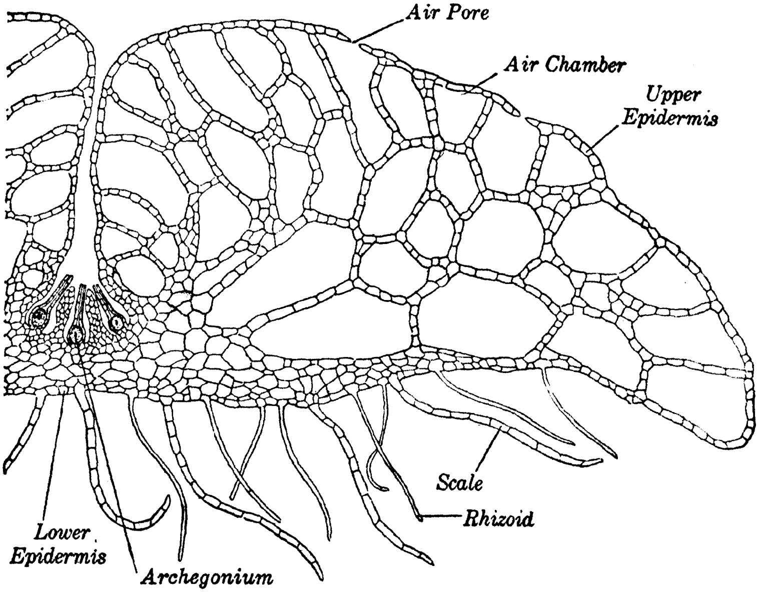


FIG. 247. Portion of a cross section of a thallus of Riccia, bearing archegonia.

attach the plant to the soil or extend into the water. Some rhizoids are smooth-walled; the walls of others have peg-like internal thickenings. The rhizoids, in their mode of origin and in their functions, resemble the root hairs of such a plant as the sunflower. Scales are more abundant on the water form, rhizoids on the land form.

246. Sex Organs. The female gamete (egg) is produced in an *archegonium*, the male gamete (antherozoid) in an *antheridium*. The archegonium of a liverwort is very different from any structure found among thallophytes. The antheridium differs from organs of the same name borne by some algae and fungi in that it possesses an outer layer of sterile cells—cells, that is, which never develop into male gametes. These organs may appear on plants of Riccia living either on the water or on land. Both archegonia and

antheridia may be borne by the same plant and even by the same branch. They are produced in three to five rows on the upper surface in or near the median line (Fig. 247), and when mature are nearly or quite imbedded in the thallus in consequence of the division and growth of neighboring cells.

Antheridia appear first on young plants; after a varying number of antheridia have been formed, the development of archegonia

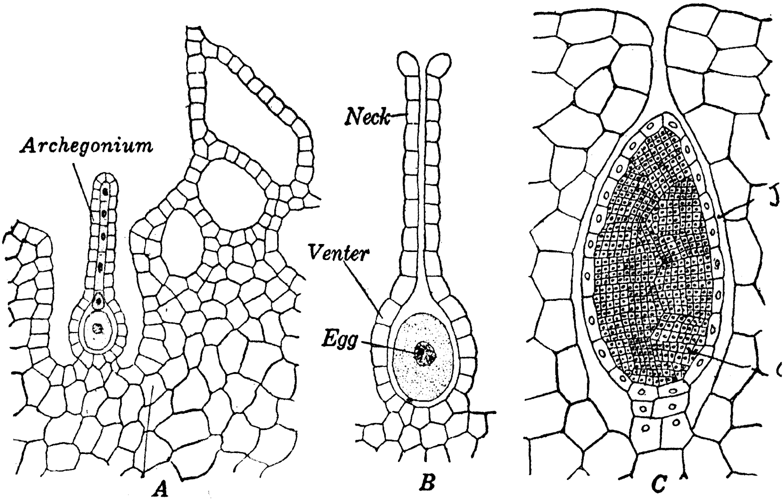


FIG. 248. Sex organs of Riccia. *A*, nearly mature archegonium with surrounding tissue. *B*, mature archegonium. *C*, antheridium with surrounding tissue.

begins. Each sex organ originates in the apical region of the thallus; hence, in a branch bearing organs of both kinds, the antheridia are on the older portion and the archegonia are nearer the apex.

An antheridium (Fig. 248, *C*) consists of a short, few-celled stalk and an ovoid body; the latter is composed of an outer layer or jacket of sterile cells and numerous internal cells which, while the antheridium is growing, undergo repeated divisions. After these divisions cease, each of the hundreds of internal cells now present develops into an antherozoid. An antherozoid has a slender, somewhat coiled body, and two long flagella attached near its anterior end. The mature antheridium is entirely enclosed within a cavity of the thallus; this cavity opens by a narrow pore at its upper end. After antherozoids are formed, if water penetrates the cavity, the sterile cells constituting the upper end of the anther-

idial jacket become softened and disintegrate, and a viscous fluid containing the antherozoids oozes out of the antheridium and through the neck of the cavity to the upper surface of the thallus. Here, if sufficient water is present, the antherozoids swim freely.

An archegonium (Fig. 248, *A*) also has a short stalk; its body is composed of an enlarged basal *venter* and a slender *neck*. Both neck and venter consist of a single outer layer of jacket cells and an inner axial row typically of six cells of which the lowest and largest, lying within the venter, is the egg. When the archegonium

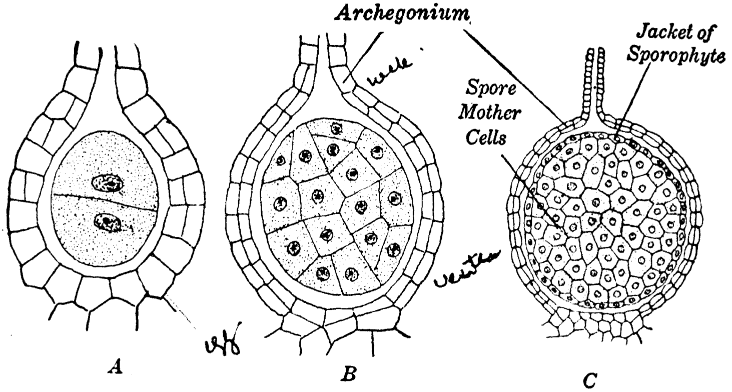


FIG. 249. Stages in the development of a sporophyte of Riccia within the venter of an archegonium. *A*, 2 cells, formed by division of the zygote. *B*, somewhat later stage. *C*, stage at which spore mother cells are present.

is mature, all the cells of the axial row, except the egg, degenerate into a mucilaginous mass; the cells at the distal end of the neck become spread apart; and a *canal* filled with the mucilaginous substance is thus formed, which extends from the open end of the neck of the archegonium to the egg (Fig. 248, *B*). The archegonium, like an antheridium, is enclosed in a cavity, but the end of its neck protrudes slightly above the surface of the thallus and into the median furrow.

247. Gametic Union. When the plant is floating, some of the freely swimming antherozoids are sure to come into the immediate vicinity of mature archegonia. If the plant is on land, a film of water must be present on its upper surface, as at the time of a rain or of a heavy dew, in order to make possible the approach of an antherozoid to an archegonium. In either case the antherozoid,

coming near the mouth of an archegonium responds to a stimulus, probably of a chemical nature, by swimming directly toward and into the archegonium and down its neck toward the egg. Several or many antherozoids may thus enter an archegonium. One of them (and usually, at least, only one) unites with the egg.

248. Sporophyte. The zygote formed by the union of egg and antherozoid secretes a new wall and begins to grow almost immediately (Fig. 249). The first division of the zygote is approximately horizontal. As a result of succeeding divisions and further growth, the zygote develops into a spherical mass of cells; the cells of the outer layer of this mass, becoming large and flat, constitute a sterile jacket. These outer cells contain chloroplasts and carry on some photosynthesis. The cells within the jacket continue to divide until there are present a large number of *spore mother cells*. These become more or less separated and rounded, and each undergoes two divisions to form four spores (Fig. 250). The spores in turn become separated and each secretes a thick wall. The simple spherical structure developed from the zygote, although

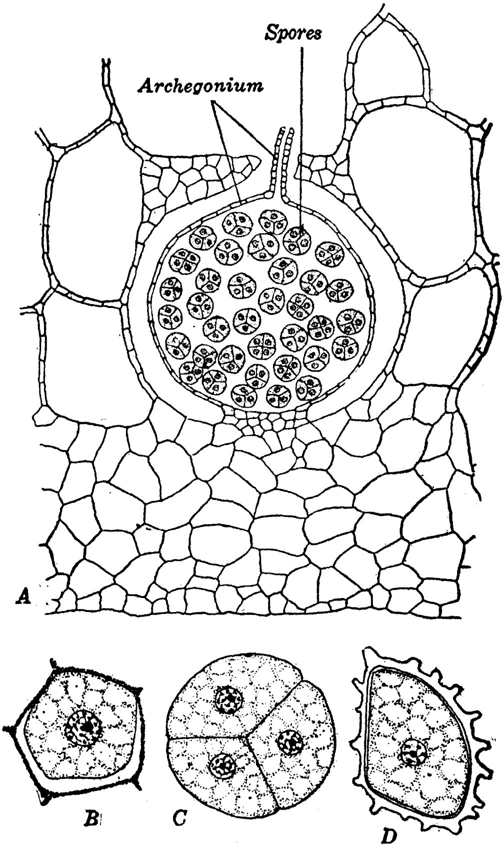


FIG. 250. *A*, nearly mature sporophyte; the mass of spores is immediately surrounded by the outer layer of cells of the venter, which is enclosed within the tissue of the gametophyte. *B*, spore mother cell. *C*, young spores (only 3 of the 4 visible) formed from a single spore mother cell. *D*, mature spore.

very small and entirely different from the plant that bore the gametes, is nevertheless a distinct plant. Since this small plant produces spores and therefore reproduces asexually, it is the *sporophyte* or asexual generation of Riccia, as distinguished from the much larger green thallose plant which bears the gametes and is therefore the *gametophyte* or sexual generation. The sporophyte, being enclosed within the tissues of the gametophyte, although

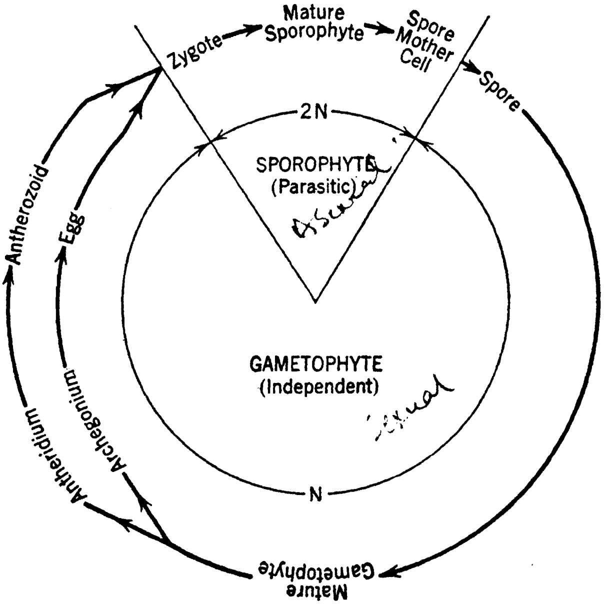


FIG. 251. Diagram of the life cycle of Riccia (or other liverwort).

its cells carry on a limited amount of photosynthesis, is largely parasitic upon the gametophyte.

The development of the zygote into a sporophyte goes on within the venter of the archegonium. As the sporophyte grows the venter also grows, continuing to enclose the sporophyte, while the neck of the archegonium withers. Very soon after the union of the gametes, the venter, at first composed of one layer of cells, in consequence of cell divisions becomes two cells in thickness. After spores are formed, the cells of the inner layer of the venter, as well as those of the jacket of the sporophyte, disintegrate. The rounded mass of spores, now surrounded only by the outer cell layer of the venter, remains imbedded in the gametophyte until

the spores are liberated by the death and decay of that part of the thallus. Each spore may then develop into a gametophyte in the manner already described.

249. Alternation of Generations. The life cycle of Riccia includes two distinct phases (Fig. 251). The germinating spore develops into a gametophyte, which bears sex organs in which gametes are produced. The union of gametes forms a zygote. The zygote develops into a sporophyte whose characteristic function is the production of spores. Each spore produced by a sporophyte may in turn develop into a gametophyte. These facts may be expressed in the following formula: Gametophyte—Gametes—Zygote—Sporophyte—Spores—Gametophyte—Gametes, etc. Each generation produces by means of its reproductive cells the other generation, hence there is an *alternation* of the two generations.

A fundamentally similar alternation of generations (that is, of gametophyte and sporophyte) characterizes the life cycles of all liverworts and of all the plants that stand above them in the evolutionary scale, as well as of many algae and fungi.

Marchantia

250. Gametophyte. From a condition, somewhat like that in Riccia, of a simple thallose gametophyte and a very simple sporophyte, evolution among liverworts seems to have taken place in several divergent directions. In one line of descent, beginning with forms more or less like Riccia and culminating in *Marchantia,* both gametophyte and sporophyte became progressively larger and more complex. The gametophyte of Marchantia presents, so far as we now know, the highest degree of complexity (though not the greatest size) ever attained by a thallose plant.

The gametophyte of *Marchantia polymorpha* (Fig. 252), one of the most widely distributed liverworts, grows on moist rocks or soil. It resembles that of Riccia in general form, as well as in its method of development from a spore, in apical growth by means of a group of embryonic cells, and in method of branching. It is, however, broader and thicker than the thallus of Riccia, and has a rather conspicuous midrib marked above by a shallow groove and below by a projecting ridge. As in Riccia, the upper surface of the thallus is divided into small rhomboidal areas (Fig. 253, *A*), each area indicating the position of an air chamber just beneath the uppermost layer of cells. The air chambers are in a single

layer (Fig. 253, *B*); each chamber opens externally by a pore which is surrounded by a chimney-like structure composed of four vertical rows of cells. In each air chamber are branching filaments of cells, growing upward from the layer of cells that compose the floor of the chamber. The cells of these filaments contain chlorophyll and constitute the chief photosynthetic tissue of the plant;

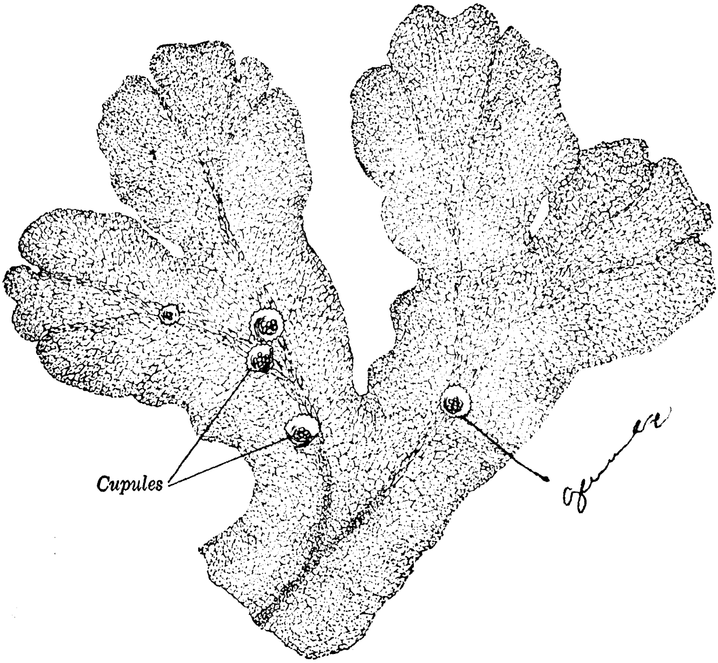


FIG. 252. Thallus of Marchantia bearing cupules in which gemmae are produced.

but there are many chloroplasts also in the cells of the layers bounding each chamber above and below, and in those of the partitions between the chambers. The portion of the thallus below the air chambers consists of several layers of cells possessing few or no chloroplasts. Many of these cells contain leucoplasts which form storage starch; in some of them are oil bodies like those of Riccia; a few large cells contain mucilage. The cells of this part of the thallus are parenchymatous, except that in the midrib are elongated cells with locally thickened walls, constituting probably a rudimentary conductive tissue. From the lower surface of the

thallus grow scales and rhizoids. Some rhizoids are smooth-walled; the inner surfaces of the walls of others are marked by localized thickenings of varied form.

251. Vegetative Multiplication. In consequence of apical growth and branching and of the progressive death of the older parts of the thallus, the number of plants is increased, just as is the case in

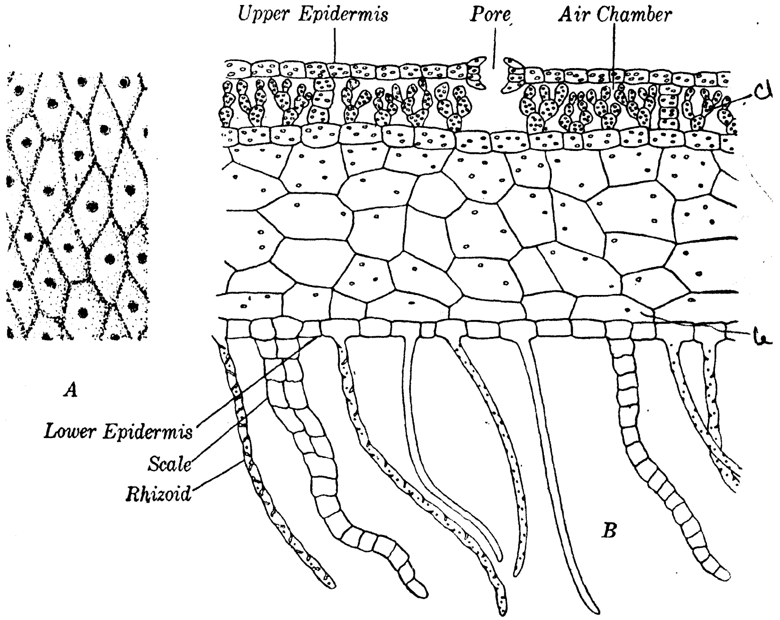


FIG. 253. Marchantia. *A*, surface view of a portion of a thallus showing rhomboidal areas, each marking the position of an air chamber. *B*, cross section of a portion of a thallus.

Riccia. Adventitious branches also may develop from almost any part of the thallus in consequence of wounds or possibly of other stimuli; and these branches, if separated by any means, become new plants. In addition, Marchantia has a means of vegetative multiplication by the formation of lens-shaped structures (*gemmae*) which are produced in great numbers in shallow cups (*cupules*, Fig. 252) on the upper surface of the thallus. Each gemma (Fig. 254) is attached to the thallus by a single-celled stalk which is easily broken. If the gemma, freed by the breaking of its stalk, comes to lie upon the soil, rhizoids develop from certain special cells of the surface in contact with the soil, and two groups of

cells located in two notches on opposite edges of the gemma begin to divide. By the division of the cells in these groups, and by the growth and division of their daughter cells, the gemma in time develops into a new plant.

252. Sexual Branches. The sex organs of Marchantia are similar in structure to those of Riccia. They are borne, however, on special upright branches (Fig. 255), each composed of a stalk and a terminal horizontal disk. Male and female branches (in *Marchantia polymorpha*, though not in some other species of Marchantia) are borne on distinct plants. It is worthy of note that the sexual distinction between plants of this species is so sharply fixed that gemmae from a male plant give rise always to male plants and those from female plants develop always into female plants. The upright sexual branches are direct continuations of the horizontal branches of the thallus; and a cross section of the stalk of a male or female branch shows the presence of tissues corresponding respectively to those of the upper and lower surfaces of an ordinary branch of the thallus.

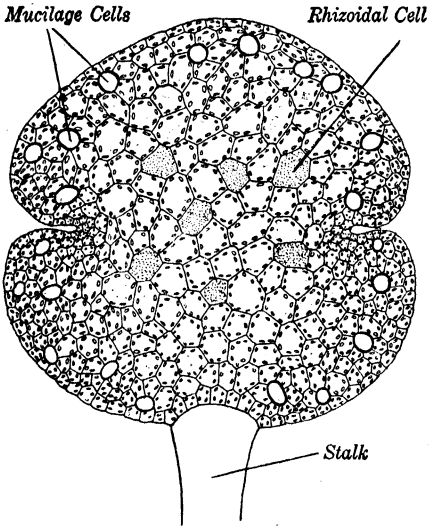


FIG. 254. A gemma of Marchantia.

The disk borne by a male branch (Fig. 256) is eight-lobed, and imbedded in the upper surface of each lobe are many antheridia, the oldest nearest the center, the youngest toward the outer extremity of the lobe. Between the cavities containing antheridia are air chambers with pores. When an antheridium is mature, contact with a drop of water causes some of the sterile cells in the upper part of its jacket to disintegrate, and the mass of antherozoids (Fig. 257) oozes out to the surface of the disk.

A female disk (Fig. 258) is inconspicuously eight-lobed, a group of archegonia being borne in an inverted position, not imbedded, on the lower surface of each lobe. However, the first-formed

Porella

254. Gametophyte. In another line of descent, beginning apparently with species whose gametophyte was even simpler than that of Riccia, evolution has resulted in an external differentiation of the thallus into stem and leaves, accompanied by little if any internal differentiation of tissues. The leafy liverworts thus produced, of which *Porella platyphylloidea* (Fig. 260, *A*, *B*) is a common

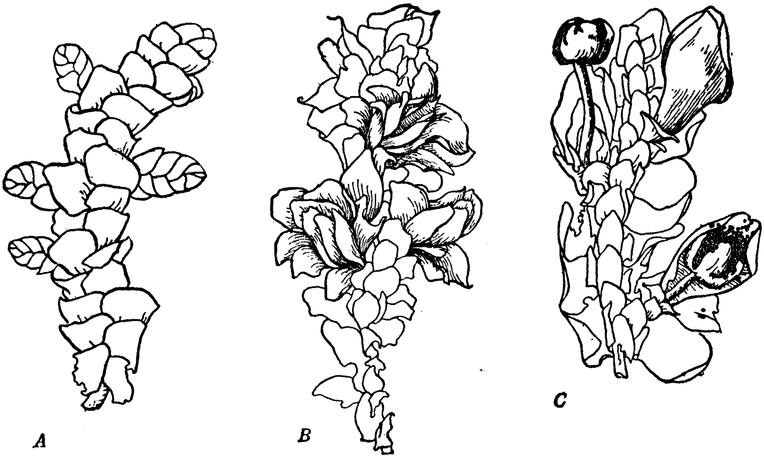


Fig. 261. Porella. *A*, male plant; antheridia are borne on the short side branches. *B*, female plant with short archegonial branches. *C*, female plant bearing sporophytes; at the upper right, a sporophyte still enclosed in a sheath; lower right, a sporophyte whose capsule has opened somewhat prematurely, freeing spores and elaters; upper left, a fully matured sporophyte with elongated stalk and emptied capsule.

example, typically have three rows of leaves. The leaves of two rows seem to have been developed in the course of evolution from lateral lobes of the thallus, the divisions between which extended almost to the median line, leaving as a central axis only a midrib or stem; the leaves of the third row seem to correspond to the scales borne on the under surface of the thallus of such a form as Riccia or Marchantia.

Porella grows most commonly on the bark of trees and on rocks, the branching plants forming close green mats. It can withstand drying, at least for several months, without apparent injury. At the growing end of the stem is a single *apical cell* (Fig. 260, *C*) instead of a group of embryonic cells such as occurs in Riccia or

Marchantia. An apical cell of Porella has the form of a triangular pyramid whose base is the free (anterior) face of the cell. From each of the three lateral faces of this cell daughter cells are formed in regular sequence, which by their division followed by divisions of their daughter cells give rise to all the cells of the plant. Each row of leaves, as well as a part of the stem, arises from the cells thus cut off from one face of the apical cell. Since cells are cut off from three faces, three rows of leaves are produced. The stem is a continuous central axis which gives rise, from time to time, to lateral branches—a method of branching very different from that which characterizes Riccia or Marchantia. Each branch has an apical cell, and its development (including the production of leaves and sometimes of secondary branches) repeats the development of the main stem. Scattered smooth-walled rhizoids, which attach the plant to the substrate, grow from the lower surfaces of stem and branches.

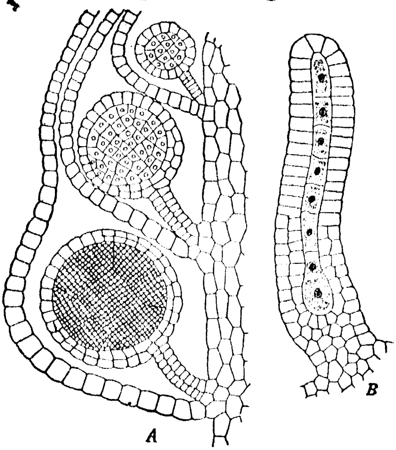


FIG. 262. *A*, portion of a branch of Porella bearing antheridia. *B*, archegonium.

Each lateral leaf has a large upper lobe and a smaller lower one; the lower lobe appears like a flap attached to the stem and to the posterior edge of the upper lobe, and turned forward under the latter. Each lobe consists of one layer of cells. When a branch is formed, it replaces the lower lobe of a leaf. On the lower side of the stem is a row of smaller leaves, also one cell in thickness. There is no differentiation of tissues in stem, branches, or leaves.

255. Sex Organs. These arise on special lateral branches, antheridial and archegonial branches being borne (in *Porella platyphylloidea*) on separate plants (Fig. 261). The male plants (those bearing antheridial branches) are in general smaller than the female (those bearing archegonial branches), but the difference is not great enough to make it easy always to determine the sex of a plant that is not producing sexual branches.

An antheridial branch is comparatively short, and its leaves are

very close together. In the axil of each leaf is an antheridium (Fig. 262, *A*) differing from an antheridium of Riccia only in that it has a long stalk and that its wall, except at the outer end, is composed of more than one layer of cells. It is not enclosed in a cavity. The antherozoids are like those of Riccia, and, as in that plant, gametic union depends upon the presence of sufficient water to enable an antherozoid to swim and to be carried to the neighborhood of an archegonium.

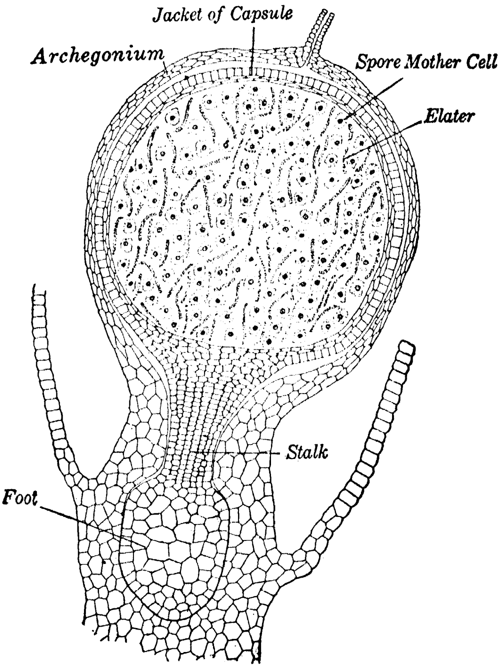


FIG. 263. Lengthwise section of a developing sporophyte of Porella, with adjacent parts of the parent gametophyte.

An archegonial branch is shorter than an antheridial branch; it bears only two or three leaves and, at its end, a group of a few archegonia. One of the archegonia is developed from the apical cell of the branch, and thus further growth of the branch is prevented. Each archegonium (Fig. 262, *B*) resembles one of Riccia except that the venter is little broader than the neck. After the archegonia reach maturity, the whole group is surrounded by a thin, cup-like sheath that has developed from the archegonial branch just below the archegonia.

256. Sporophyte. The sporophyte of Porella (Fig. 263) is similar to that of Marchantia in being composed of foot, stalk, and capsule. As in Marchantia, the stalk elongates when the spores are mature, pushing the capsule well out beyond the enclosing sheath.

The jacket of the capsule consists of two or more layers of cells.

In the interior of the capsule are produced, as in Marchantia, spores and elaters. When the elongating stalk has pushed the capsule beyond the sheath, the capsule wall splits from its apex to near its base into four parts, liberating the spores. Each spore may develop into a new gametophyte.

FIG. 264. Gametophyte of Anthoceros bearing sporophytes.

ANTHOCEROS

257. Gametophyte. A third type of evolutionary development among liverworts is illustrated by *Anthoceros* (Fig. 264). In this plant it is the sporophyte which shows the most marked advance over a primitive condition. The gametophyte is small and irregularly and inconspicuously branched. It has no differentiated tissues and no air chambers, but has intercellular spaces opening to the lower surface of the thallus. Some of these spaces are filled with a mucilage-like substance; in others are colonies of a blue-green alga (Nostoc). Antheridia (Fig. 265) develop in groups, each group in an internal cavity beneath the upper surface of the thallus. The layers of cells forming the roof of this cavity are finally broken by the growing antheridia. Archegonia (Fig. 266) develop separately rather than in groups and are closely imbedded in the upper surface of the thallus, only the extreme ends of their necks protruding. The venter and neck of each archegonium are continuous with the surrounding cells of the thallus.

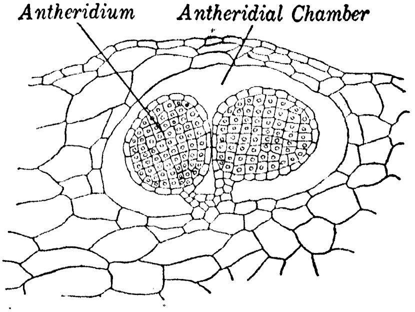


FIG. 265. Portion of a thallus of Anthoceros in vertical section, showing 2 enclosed antheridia.

258. Sporophyte. A young sporophyte consists of a foot, a very short stalk, and a capsule. The capsule is characterized by the presence of an embryonic region at its base, in which cell division continues for a long time. Consequently, the capsule grows into

the bogs in which Sphagnum grows, these dead organic substances are not completely decomposed by the bacteria that cause decay. Chemical changes other than decay result in the formation of the spongy, dark-colored substance known as peat. Further changes in the peat may in the course of long periods of time lead to the production of certain types of coal.

At the growing end of the stem and of each branch is an apical cell, resembling in shape and function the apical cells of the mosses already described. As in other mosses, leaves are formed in three rows; but as the stem and leaves grow, the latter become displaced and lose their three-ranked arrangement. While very young, a leaf consists of a single layer of cells, all similar (Fig. 280, *A*); but as the leaf matures, these cells become differentiated (Fig. 280, *B–D*). Alternate cells grow both in length and in breadth and ultimately die, leaving only their walls. These large cells are frequently characterized by spiral and ring-shaped thickenings on the inner surfaces of their walls, and often the walls are perforated, the pores being variable in size and shape. Between these large cells and forming a network are other cells which grow chiefly in length, remain alive, and retain chlorophyll. Large dead cells like those

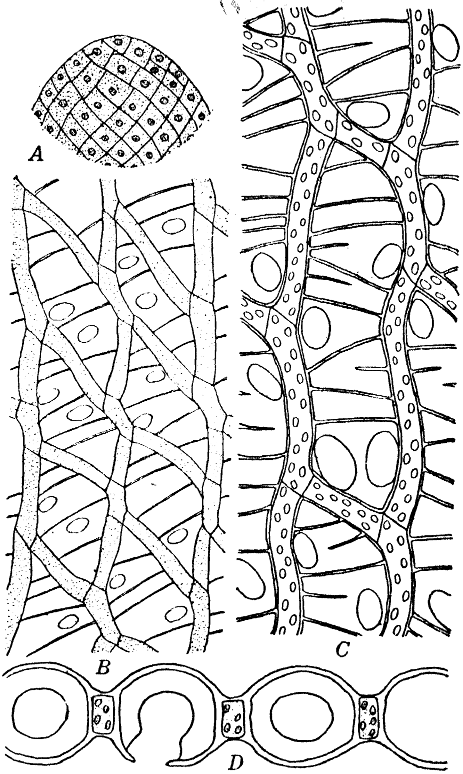


FIG. 280. Development of a leaf of Sphagnum. *A*, tip of a young leaf, its cells still embryonic. *B*, *C*, portions of leaves at later stages (*C* at maturity), showing the differentiation of 2 types of cells. *D*, portion of a cross section of a mature leaf; small green cells alternate with large dead ones.

in the leaves occur in the cortices of the stems and branches of a few species. Cells of this character in leaf and stem play an important part in the absorption and retention of water. The stem and branches, except in species that grow submerged in water, possess mechanical tissues also.

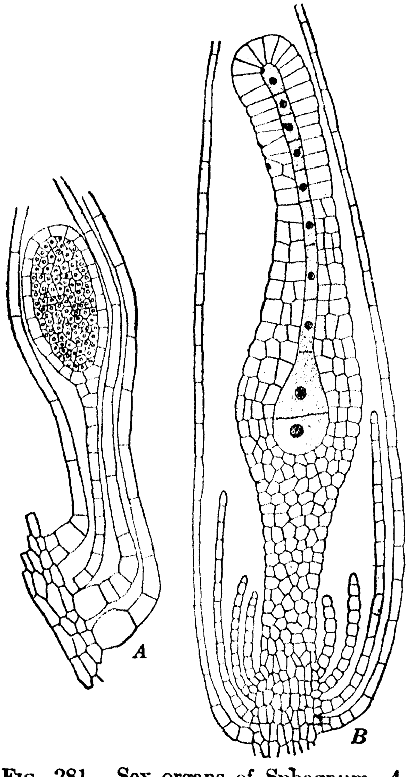


FIG. 281. Sex organs of Sphagnum. *A*, portion of an antheridial branch with an antheridium. *B*, apex of an archegonial branch; the archegonium enclosed by leaves.

266. Sex Organs. Antheridia and archegonia (Fig. 281) are produced usually in late summer and early fall on short branches borne near the apex of the stem. The antheridial and archegonial branches may, according to the species, be borne on the same plant or on separate plants; but antheridia and archegonia never occur on the same branch. The leaves on an antheridial branch are often brown, purple, or red, even in those species the leaves on whose other branches are green. An antheridium resembles one of Porella (Fig. 262, *A*), and as in Porella each antheridium is borne in the axil of a leaf.

The very short archegonial branches are closely crowded at the apex of the stem. One archegonium is developed from the apical cell of each branch, and several other archegonia may be formed about the base of the first. In cold countries the sex organs pass the winter under the snow, and gametic union occurs in the spring at the time of the melting of the snow and ice.

267. Sporophyte. A mature sporophyte of Sphagnum (Fig. 282) consists of a bulb-like foot which is imbedded in the tissues of the branch beneath the archegonium; a terminal capsule, al-

most spherical in shape, within which are borne spores; and a very short stalk that is hardly more than a constriction between foot and capsule. The spores are formed in a relatively thin, dome-shaped zone in the upper part of the capsule. When the spores are nearly mature, a portion of the branch beneath the foot of the sporophyte elongates and carries the sporophyte beyond the enveloping leaves. A dome-shaped lid is formed at the apex of the capsule. The lid is thrown off by an explosive action of the capsule, which also ejects the spores.

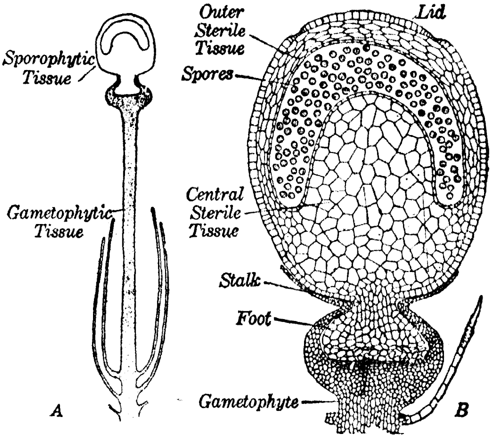


FIG. 282. *A*, diagram of the apical portion of a leafy shoot of Sphagnum bearing a sporophyte. Note especially the elongation of the upper portion of the gametophytic tissue (shaded) that pushes the sporophyte (unshaded) above the surrounding leaves. *B*, lengthwise section of a nearly mature sporophyte.

268. Uses of Sphagnum. The part played by Sphagnum plants in the formation of peat and of some kinds of coal has already been mentioned. Dried peat is used in various countries as a fuel. During the World War, Sphagnum came into wide use as a material for surgical dressings. It had, indeed, been used for centuries in the dressing of wounds in Scotland, Ireland, and some parts of northern Europe, and was extensively employed for first-aid purposes by the Japanese during the Russo-Japanese War. The great advantage of Sphagnum for this purpose is its capacity for absorbing liquids; a mass of Sphagnum of one of the species best adapted to surgical use may absorb from 15 to 20 times its own weight of water.

Sphagnum is much used in the packing of live plants which are to be shipped. Its value for this purpose lies also in its ability to absorb moisture and to retain it for a considerable time.

269. Distinctive Features of Bryophytes. Liverworts and mosses together constitute the division known as *bryophytes*. About 9,000

species of liverworts and 13,500 species of mosses are now recognized.

Although conspicuous differences distinguish various liverworts and mosses, their relationship is clearly shown by a close similarity throughout the division in the form and structure of sex organs and gametes. Both antheridium and archegonium are characterized by the presence of an outer layer of sterile cells. In this respect the gamete-producing organs of a bryophyte differ from the corresponding organs of any thallophyte.

Liverworts and mosses are alike also in having an alternation of generations; the gametophyte is, in every case, the larger, longer-lived, independent generation; the sporophyte is smaller, shorter-lived, and parasitic upon the gametophyte. While an alternation of generations occurs in many thallophytes (algae and fungi), in no alga or fungus are the relations between gametophyte and sporophyte closely comparable to those existing between the two generations of a bryophyte.

The bryophytes display a high degree of sexual differentiation, marking a great advance over the primitive form of gametic union which occurs in Chlamydomonas, in which the two gametes that unite are, to all appearances, alike. In various lines of evolution among plants, a differentiation has appeared between the gametes. Some of the steps in this type of evolutionary development are illustrated by algae and fungi described in previous chapters. One type of gamete performs especially the function of storing food to be used by the zygote and, in many-celled forms, by the young plant (embryo) which will develop from the zygote; in adaptation to its function, this gamete, now called the female gamete, has become larger and has lost the power of movement. The male gamete, on the other hand, retains the power of movement, which is essential to its union with the female gamete; and, relieved of the necessity of food-storage, it has become smaller and better adapted to rapid movement. The female gamete (egg) and the male gamete (antherozoid) of a bryophyte have thus come to be very different in size and structure, the antherozoid being reduced to little more than a nucleus and a pair of flagella.

This differentiation of gametes into two sorts, each adapted to a particular function, is the basis of what is commonly known as *sex* in both plants and animals. Sexual differentiation extends in the bryophytes also to the production of distinct organs (archegonium

and antheridium) in which the respective gametes are produced; and in a number of liverworts and mosses it has extended to a differentiation in size or in external form between the female gametophyte, which produces only eggs, and the male gametophyte, which produces only antherozoids. In some species the male gametophyte is much smaller than the female gametophyte.

CHAPTER XXV

REDUCTION OF THE NUMBER OF CHROMOSOMES

270. Chromosome Numbers and the Alternation of Generations. The number of chromosomes in each cell of the gametophyte of a liverwort or of a moss may conveniently be represented as n. The numerical value of n is different for different species; for example, in some common mosses n equals 6, that is, each cell of the gametophyte contains six chromosomes. When any nucleus of the gametophyte divides, by the process described in Chapter XII, each parent chromosome is divided and its daughter chromosomes pass to the respective daughter nuclei; hence the chromosome number in each daughter cell is the same as that in the parent cell. Every cell throughout the life of the gametophyte, then, contains n chromosomes, and consequently each gamete (egg or antherozoid) which is produced by this plant has n chromosomes.

The union of the gametes involves a union of their cytoplasm and of their nuclei, but not of their chromosomes. Therefore the zygote nucleus contains n chromosomes that were contributed by the egg plus n chromosomes contributed by the antherozoid—in all, $2n$ chromosomes.

The zygote, with $2n$ chromosomes, is the starting-point of the sporophytic generation. When the zygote nucleus divides, each of its chromosomes divides; each daughter cell, therefore, formed by the division of the zygote receives $2n$ chromosomes. In the nuclear divisions which follow during the development of the sporophyte, each parent chromosome is divided and each of its daughter chromosomes passes to one daughter nucleus; hence each cell of the sporophyte has $2n$ chromosomes. Therefore, one fundamental difference between gametophyte and sporophyte is the presence in the two generations of different numbers of chromosomes—respectively n and $2n$. In a moss each cell of whose gametophyte contains 6 (n) chromosomes, each cell of the sporophyte would contain 12 ($2n$) chromosomes. Among the values of n found in

various species of mosses are 6, 8, 10, 12, 16, 20, and 32. In *Riccia natans*, n equals 9; in *Marchantia polymorpha*, n likewise equals 9. In plants of other groups the value of n ranges from 3 ($2n$ being 6) to as high as 100 ($2n$ being 200).

271. Reduction of the Chromosome Number. The doubling of the number of chromosomes each time two gametes unite would result, if nothing occurred to prevent, in a continuous increase in the chromosome number. It is clear that such an accumulation of chromosomes from generation to generation could not long continue. As a matter of fact, there is no such accumulation, because in each life cycle, at some point between one gametic union and the next, the chromosome number is reduced by one half (that is, from $2n$ to n). In liverworts and mosses and in the plants above them in the evolutionary scale, the reduction of the chromosome number is brought about in the two successive nuclear divisions that occur when a spore mother cell is divided to form four spores (Fig. 276, *D–F*). The spore mother cell, when it was formed, like any other cell of the sporophyte received $2n$ chromosomes from its parent cell; but in the divisions of the spore-mother-cell nucleus and of its daughter nuclei, the chromosome number is reduced to n. These two nuclear divisions are different, therefore, from all other divisions in the life of the plant. Since each spore, possessing n chromosomes, is the starting-point of a gametophyte, each cell of the gametophyte has n chromosomes.

This history of the chromosomes may be summed up by saying that in the union of gametes—the point of transition from gametophyte to sporophyte—the chromosome number is doubled (from n to $2n$); and that in spore-formation—the point of transition from sporophyte to gametophyte—the chromosome number is reduced (from $2n$ to n).

272. First Reduction Division (Fig. 283). In all cases in which the process has been fully studied, reduction is brought about in the course of two successive nuclear divisions, often called *reduction divisions*. The history of these divisions seems to be similar, in essential respects, in all plants and animals in which a reduction in chromosome number occurs.

When the first reduction division begins (for example, in the spore mother cell of a moss), the nucleus possesses the $2n$ chromosomes which it received from its parent nucleus. But in the early stages of this division an event occurs which does not take place

in any other division—namely, the chromosomes present in the nucleus come into contact in pairs, side by side (Fig. 283, *C*).

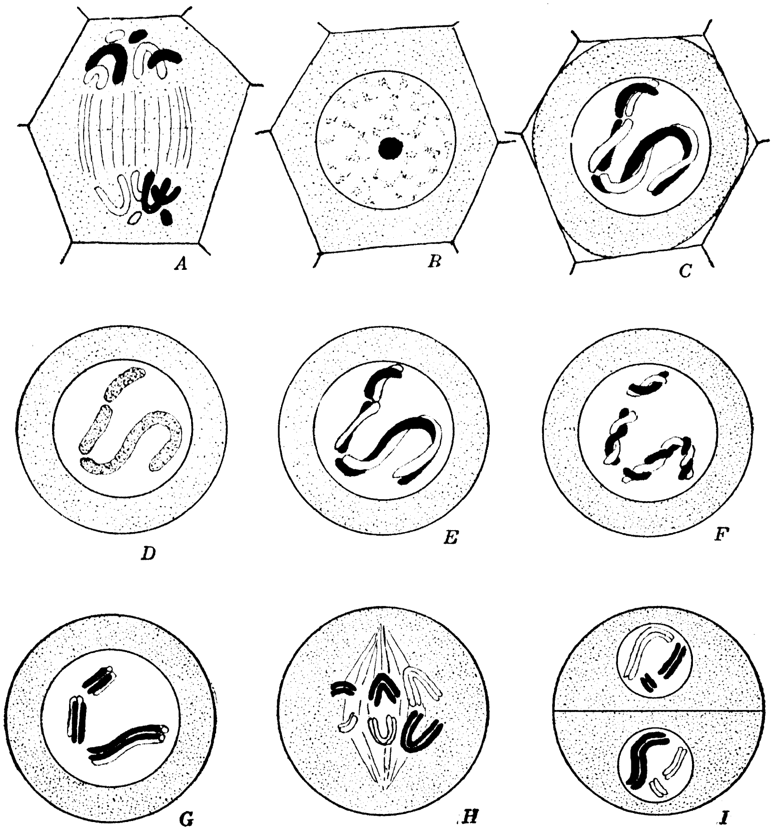


FIG. 283. Diagrams illustrating the formation of spore mother cells and the first reduction division. *A*, division by which spore mother cells are formed; 2 *n* chromosomes pass to each daughter nucleus (*n* being considered as 3). *B*, spore mother cell; nucleus in the resting stage. *C*, pairing of chromosomes; *n* pairs are present. *D*, the chromosomes of each pair in intimate contact. *E*, paired chromosomes are again visibly separate. *F*, the chromosomes have contracted. *G*, the chromosomes are now plainly split. *H*, separation of whole (but split) chromosomes after the equatorial-plate stage. *I*, the 2 daughter cells, each containing *n* split chromosomes.

It will be recalled (§ 119) that in an ordinary nuclear division the chromosomes appear to be double at an early stage, and that there are indications that the double condition is the result of a

splitting which occurred late in the course of the preceding division. There is evidence, also, that at a very early stage in the first reduction division each chromosome is similarly double (or split). The split nature of the chromosomes, however, can be made out in the early stages only in specially prepared sections of the dividing nuclei and at very high magnifications (see Fig. 397, *A*, *B*). Consequently the usual appearance, as shown in Figure 283, *C–F*, is that it is whole (that is, unsplit) chromosomes which are pairing. In these early stages, at least in many plants, the chromosome pairs are arranged end to end.

For a time the pairing of the chromosomes is so close that they often seem to be completely united; the appearance then is that of a series of single chromosomes (Fig. 283, *D*). Later the paired chromosomes separate slightly (Fig. 283, *E*). They become shorter and the end-to-end arrangement, if previously present, disappears (Fig. 283, *F*).

Sooner or later each chromosome of every pair seems to become split lengthwise (Fig. 283, *G*). From what has already been said, it is evident that this apparent splitting is really a reappearance of the doubleness which characterized each chromosome at a much earlier stage. The nucleus now contains what appear to be n chromosomes each split into four parts, but are in reality $2n$ chromosomes (in pairs) each split into two parts.

After the spindle is formed, the pairs of split chromosomes become so arranged in the equatorial plate that when later they are divided into two groups, one split chromosome of each pair is drawn to one pole of the spindle and the other of the pair is drawn to the opposite pole. In consequence, each daughter nucleus receives n longitudinally split chromosomes; the number of chromosomes has actually been reduced. This nuclear division is followed (in a moss) by a division of the spore mother cell.

273. Second Reduction Division (Fig. 284). The lengthwise split that appeared in each chromosome in the early stages of the first reduction division was in preparation for the *second* division. This division follows very soon after the first; so soon, in many cases, that the daughter nuclei of the first division have not time to pass into a resting condition. A new spindle is formed for the division of each of these two nuclei. The chromosomes of each nucleus become arranged in an equatorial plate on one spindle, and the halves of each split chromosome pass to opposite poles.

Thus four daughter nuclei are formed, each with *n* chromosomes. Nuclear division is again followed by cell division, as a result of which each of the four nuclei formed by the second division becomes the nucleus of a spore. Therefore, by means of two divisions, four spores each with *n* chromosomes have been formed from the spore mother cell which had 2 *n* chromosomes.

274. Some Effects of the Reduction Divisions. One obvious effect of these two nuclear divisions is to reduce the number of chromosomes from 2 *n* to *n*. Perhaps more important, however,

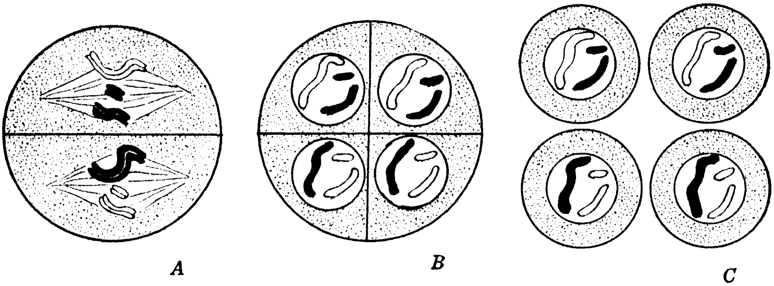


FIG. 284. Second reduction division. *A*, equatorial-plate stage. *B*, completion of the second division; each of the 4 spores contains *n* chromosomes. *C*, separation and rounding up of spores.

is the fact that during the reduction divisions *new combinations* of chromosomes are brought about.

The nucleus of a moss zygote (or of the zygote of any other plant or animal) contains 2 *n* chromosomes: *n* chromosomes which are *maternal* because they were contributed by the egg; and *n paternal* chromosomes which were contributed by the male gamete. When the zygote nucleus divides, each of its daughter nuclei receives one half of each maternal, and one half of each paternal, chromosome; each daughter nucleus, therefore, like the zygote nucleus, has *n* maternal and *n* paternal chromosomes. Since a splitting and a division of each chromosome occur in the course of each succeeding nuclear division, the nucleus of every cell of the sporophyte, to and including the spore mother cells, has *n* maternal and *n* paternal chromosomes.

When the chromosomes become paired in the early stages of the first reduction division in a spore mother cell, each pair is composed of one maternal and one paternal chromosome which in some way correspond each to the other. When the chromosomes of any pair

pass to the respective daughter nuclei, it is a matter of chance which daughter nucleus receives the maternal, and which the paternal, chromosome of that pair. If one daughter nucleus receives the maternal chromosome of one pair and the paternal chromosome of a second pair, the other daughter nucleus will receive the paternal chromosome of the first pair and the maternal chromosome of the second. Hence new chromosome combinations result. If the parents differed in numerous characters, as is ordinarily the case, then, since chromosomes carry substances concerned in inheritance, each maternal chromosome is likely to differ somewhat in constitution from the paternal chromosome of the same pair. In such a case the nuclei formed by the first reduction division, and ultimately the spore nuclei formed by the second division, will be of different kinds with respect to the inheritance which they will pass on to the next generation. The processes that occur in the course of the reduction divisions help, therefore, to explain how it comes about that offspring differ from their parents, and that offspring of the same parents differ from one another.

Not only are new combinations of *whole* chromosomes brought about in the way just described; it appears that in the course of the reduction divisions new combinations of *parts* of chromosomes may be effected. Present evidence indicates that during the close side-by-side association of paired chromosomes in the early stages of the first reduction division, an interchange of material may occur (see also Chap. XXXII). Therefore, when the paired chromosomes separate, the maternal one of any pair may contain some substances of paternal origin, and the paternal chromosome may contain some of maternal origin. Such interchanges between chromosomes evidently greatly increase the possibility of the appearance of different combinations of characters in the spores and in the plants to which the spores will give rise.

275. Chromosome Reduction in Thallophytes. In bryophytes (liverworts and mosses) and in the plants that stand above them in the evolutionary scale (pteridophytes and seed plants), the reduction of the chromosome number occurs regularly at the same stage in the life cycle—namely, in the division of the nucleus of a spore mother cell. The plants of these higher groups agree, therefore, in possessing a sporophytic generation characterized by the presence of 2 n chromosomes and a gametophytic generation each of whose cells has n chromosomes.

Among thallophytes, however, there are great differences between different classes with respect to the stage at which the chromosome number is reduced. In several green algae, for example, it has been shown that chromosome reduction occurs in the division of the zygote nucleus and of its daughter nuclei. This is the case in Volvox, Ulothrix, and Oedogonium, and almost certainly in Chlamydomonas. In such an alga the zygote is the only cell possessing 2 *n* chromosomes, and there is no generation corresponding to the sporophyte of a moss. In Spirogyra, similarly, chromosome reduction is effected in the two divisions that occur shortly after gametic union. Of the four nuclei, each with *n* chromosomes, formed from the zygote nucleus by these divisions, it has been seen that three nuclei degenerate. Hence the single nucleus present in the zygote of Spirogyra during its later history has but *n* chromosomes. The filament resulting from the germination of the zygote consists of cells with *n* chromosomes each—that is, it is a gametophyte. Spirogyra, like Volvox, therefore, has no sporophytic generation. In some other green algae, including certain species of Cladophora and Ulva, there is a true alternation of generations.

The brown algae possess an alternation of generations comparable with that in bryophytes and higher plants. In some brown algae, including Ectocarpus, the gametophyte and sporophyte are alike except for their reproductive structures. In other brown algae the two generations are very dissimilar in size and structure. For example, the sporophyte of Laminaria is a large, complex plant and the gametophyte is small and simple. Reduction of the gametophyte is carried to an extreme in Fucus, whose sporophytic (2 *n*) generation is practically the whole plant. Chromosome reduction in Fucus occurs in the first two nuclear divisions in oögonium and antheridium respectively; the gametophyte is represented, therefore, only by the four- and eight-nucleate stages in the oögonium and by the four-nucleate and succeeding stages in the antheridium.

In the majority of red algae also, including Polysiphonia, there is an alternation of generations. The plant of Polysiphonia which bears gametes is a gametophyte, with *n* chromosomes in each cell; the sporophytic generation, beginning with the zygote, includes the branches that give rise to carpospores, the carpospores themselves, and the plant that bears tetraspores. Chromosome reduc-

tion occurs in the divisions that form the tetraspore nuclei. On the other hand, Nemalion and some other red algae possess only a gametophytic generation; as in some green algae, the chromosome number is reduced in the first and second nuclear divisions after gametic union. These divisions, in Nemalion, occur when the zygote germinates.

Differences appear among fungi as great as those among algae with respect to the time of chromosome reduction.

In Rhizopus, chromosome reduction is probably effected during some of the nuclear divisions that occur at the time of, or shortly after, the germination of the zygote. The particular divisions with which chromosome reduction is connected have not, however, yet been certainly recognized.

In the ascomycetes (with perhaps some exceptions) the chromosome number is reduced by the first two nuclear divisions in the ascus.

Among basidiomycetes, chromosome reduction is brought about in the rusts (again with possible exceptions) by the two nuclear divisions in the germinating teleutospore; in smuts, probably by two divisions in the germinating winter spore; and in mushrooms, by the two nuclear divisions in the basidium.

276. Relation of Chromosome Reduction to Gametic Union. A knowledge of the steps in the reduction of the chromosome number throws some additional light upon the real nature and significance of gametic union. The pairing or conjugation of chromosomes that takes place early in the first reduction division is the final step in a history that began with the union of gametes. Every case of gametic union, then, involves three steps:

(*a*) The union of cells.

(*b*) The union of nuclei.

(*c*) The pairing or conjugation of chromosomes.

Since the conjugation of the chromosomes may result in a redistribution of chromosomes, and to some extent in a redistribution of parts of chromosomes, one of the important consequences (if not *the* important consequence) of a gametic union is this ultimate redistribution, with the result that new combinations of inherited qualities may appear. In other words, the union of gametes, because it results finally in chromosome conjugation, is a means of securing variation (in the sense of a new grouping of inherited qualities) in plants and animals.

In the different plants thus far described, steps *a*, *b*, and *c* are separated from one another in different degrees. In Spirogyra, the union of cells (step *a*) is followed closely by the union of nuclei (step *b*), and this very soon by the conjugation of chromosomes (step *c*). In the wheat rust, there is a long period (represented by the aecidiospores, the mycelium in the wheat, and the uredospores) between steps *a* and *b*; step *b*, however (taken during the maturing of the teleutospore), is followed as soon as the teleutospore germinates by step *c*. In bryophytes and higher plants, steps *a* and *b* are close together in time, and a long gap (represented by the sporophytic generation) occurs between steps *b* and *c*.

CHAPTER XXVI

FILICINEAE (FERNS)

277. Ferns and Their Distribution. The division *pteridophytes* includes the ferns, together with the plants of certain other classes which stand more or less nearly at a common level of development. Like mosses, ferns are widely distributed. Some grow in the crevices of rocks and on the faces of cliffs where they find a scanty foothold; others in fields and open woods; but most of them thrive best in damp, shady places. In the tropics ferns are often particularly abundant, both in number of individuals and in number of species. It is in the tropics also that the largest ferns are found. These are tree ferns (Fig. 285), with erect cylindrical stems which may reach a height of 40 feet or more, each bearing at its apex a crown of widespreading compound leaves. In temperate regions most ferns have underground stems which bear slender roots and aërial leaves.

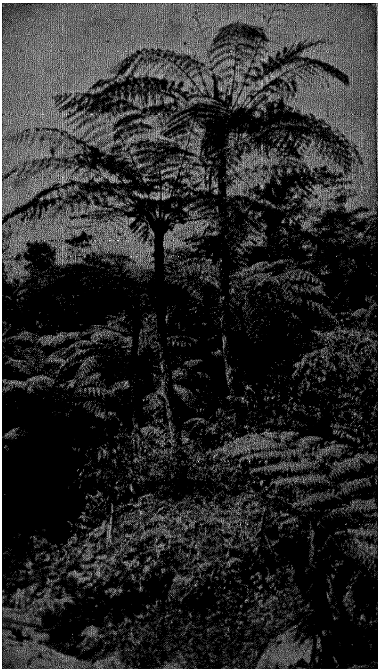


FIG. 285. Tree ferns (*Alsophila glauca*) in the Taiping Hills, Federated Malay States. After Campbell.

THE BRACKEN

278. Sporophyte. Among the common ferns living in temperate regions is a group of very similar species all generally known as the *brake* or *bracken.* The bracken of eastern North America is *Pteridium latiusculum* (Fig. 286). It grows in woods or clearings

and is particularly abundant in sandy regions. In some parts of the world brackens form dense undergrowths. The plant which consists of stem, leaves, and roots is the sporophyte. Since the stem is entirely underground, the only parts that appear above the soil are leaves. In most regions of the United States the leaves of brackens are relatively small, rarely attaining the height of a man; but those of the bracken growing in the moist, rich soils of the forests of western Washington and Oregon may reach twice that height. In Australia, bracken leaves commonly grow 10 to 12 feet high, and some 14 feet in height have been reported from the Andes.

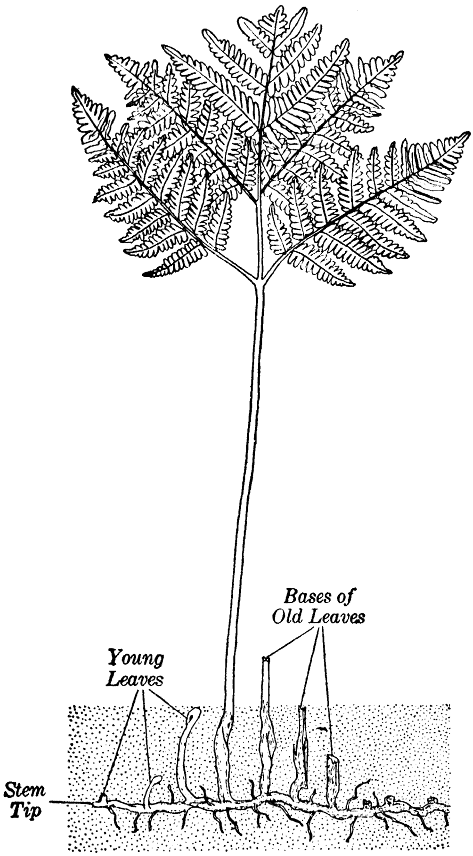


FIG. 286. The bracken.

279. Stem. The stem of Pteridium is long and slender, branching occasionally, and growing horizontally a few inches beneath the surface of the ground. Growth occurs at the anterior end, new cells being formed by division of a single apical cell; the older tissues at the posterior end in time die. When the progressive death of the older parts of the stem extends to a point at which branching has occurred, the branch becomes separated from the main stem and continues its development as an independent plant. This process is one of the means by which the number of plants is increased.

The outermost layer of the stem (Fig. 287) is an epidermis of

thick-walled cells, next within which is a sheath of mechanical tissue several cells in thickness. The greater part of the interior of the stem consists of parenchymatous cells which often contain an abundance of starch grains. Near the center of a section cut through an internode are two well-defined strands of mechanical tissue. Between these strands, in the central part of the stem, are

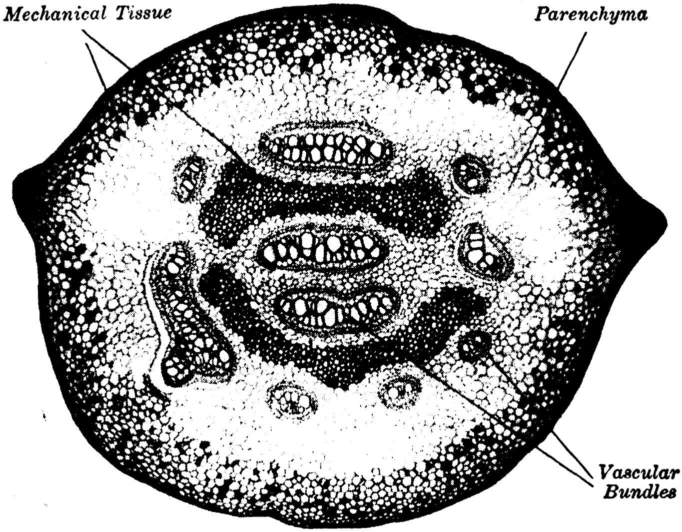


FIG. 287. Cross section of the underground stem of the bracken.

usually two vascular bundles; and in a zone outside the strands of mechanical tissue are a variable number of vascular bundles some of which are relatively small. Each vascular bundle (Fig. 288) is surrounded by an endodermis, just within which are one or two layers of pericyclic cells. The phloem lies next within the pericycle and entirely surrounds a central xylem. There is no cambium between xylem and phloem. The vascular bundles are approximately parallel through the internodes, but at each node some of them unite and new branch bundles are given off. Most of these branch bundles extend through the next internode, but some of the branches from the outer bundles pass into roots, and some from both outer and inner bundles pass into leaves. Thus the system of vascular bundles forms a network connecting all parts of the plant.

280. Roots. The roots of the bracken are small, slender, and sparingly branched. The growing end of each root is covered by a

root cap, and, as in the case of the stem, new cells arise at the growing end by division of a single apical cell. A short distance back from the root cap is a region in which root hairs occur. A cross section of a root in the mature region shows tissues generally similar in structure and arrangement to the primary tissues in a root of the sunflower (Fig. 17). However, fern roots are incapable of secondary thickening since no cambium is formed.

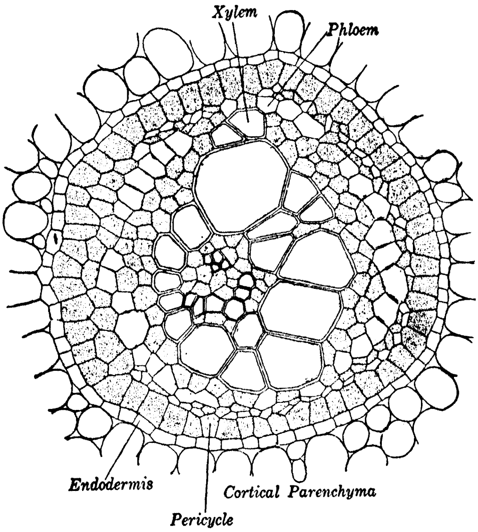


FIG. 288. Cross section of a vascular bundle of the bracken stem.

281. Leaves. On a mature plant, each leaf begins its development as a small swelling of the embryonic region at the apex of the stem. The early development of a young leaf, therefore, occurs underground; in time, an elongation of the petiole pushes the coiled upper portion of the leaf through the soil into the air. The leaf then, in a manner characteristic of fern leaves, unrolls from base to tip. A fully developed leaf (Fig. 286) consists of a slender petiole and a much-divided blade. Borne upon the central axis of the blade are two rows of primary leaflets, the basal pair being much the largest. Several pairs of the lower primary leaflets may themselves be divided, but the smaller upper primary leaflets are usually undivided. The internal structure of a leaflet resembles in most respects that of a leaf of the sunflower, having an upper and a lower epidermis, a palisade layer, spongy tissue, and veins. Stomata are abundant in the lower epidermis.

282. Sporangia. All the leaves of the bracken are green and carry on photosynthesis. Many of them also bear sporangia. A leaf bearing sporangia, whether or not it manufactures foods, is a *sporophyll.* Although all the leaves of the bracken are similar in general appearance, some of them are not sporophylls, that is,

they do not produce sporangia. On the under side of each leaflet of a sporophyll and near each edge a narrow ridge develops from whose surface grow many sporangia (Fig. 289). This ridge and

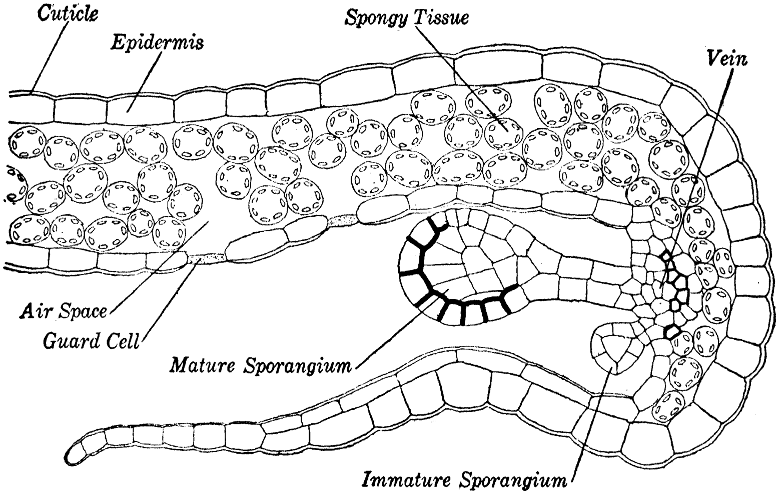


FIG. 289. Cross section of a portion of a bracken leaf, showing sporangia covered by the curved margin of the leaf.

the sporangia that it bears are covered by the curved margin of the leaflet. Each sporangium (Fig. 290) consists of a slender stalk and a capsule. The outer layer of cells of the capsule constitutes a jacket. Within the jacket, as a result of a series of divisions, spore mother cells are formed. Each spore mother cell by two further divisions produces, as in a moss, four spores. In these last two divisions, as in the corresponding divisions in a moss, the chromosome number is reduced. All the cells of the jacket are thin-walled except those of one row. Each of the cells composing this row has thick walls on all sides but the outer one. This row of cells, extending from the base of the capsule up one side, over the top, and partly down

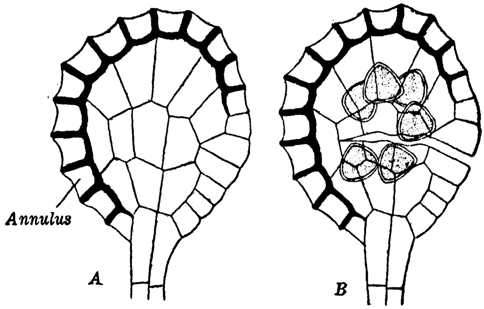


FIG. 290. Mature sporangia, closed (A) and open (B).

the other side, is the *annulus*. When the spores are mature, the cells of the jacket are dead and dry. The cell walls of the annulus are sensitive to changes in moisture. As a result of such changes the annulus straightens, breaking open the capsule, and then snaps forward. In this latter movement most of the spores are thrown out.

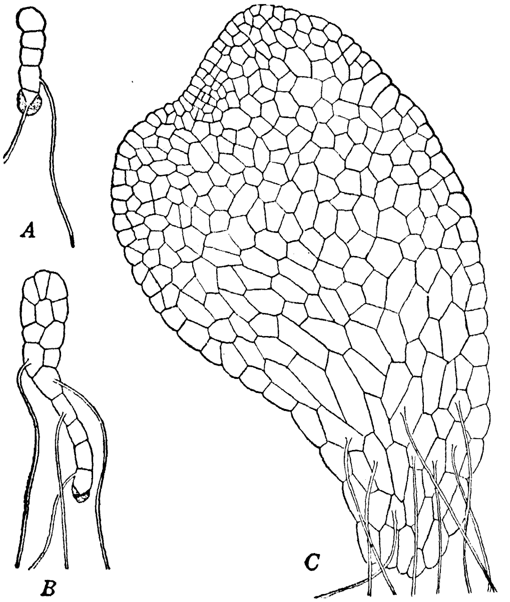


FIG. 291. *A*, *B*, early stages in the development of a prothallium from a fern spore. *C*, half-grown prothallium.

283. Gametophyte. The spores of the bracken ripen and are shed in late summer. Each spore is approximately tetrahedral in shape, and its wall has two layers: the inner one thin, the outer hard, brown, and irregularly thickened. When a spore germinates, the thick outer layer of the wall breaks, and the protoplast, surrounded by the inner layer of the wall, forms a short, green outgrowth from which a colorless projection, the first rhizoid, grows. As a result of growth and of cell divisions in one plane, the green outgrowth becomes, usually, a row of three or four cells (Fig. 291, *A*). By subsequent growth and by cell divisions in two planes, the young plant, except for the few cells nearest the old spore wall, is transformed into a flat, green plate one cell in thickness. If this small *prothallium* is not crowded during its further growth, it develops typically into a heart-shaped plant with a shallow notch at its anterior end (Fig. 291, *C*). A mature prothallium (Figs. 292, 293) is one cell in thickness, except that in a region back of the apical notch a cushion several cells thick is formed. From various cells of the under surface of the plant, and particularly in the older portion (that farthest from the notch), slender, colorless rhizoids grow out which anchor the plant and absorb

water and other materials from the soil. Prothallia may reach maturity in a few months, but they remain so small that they are

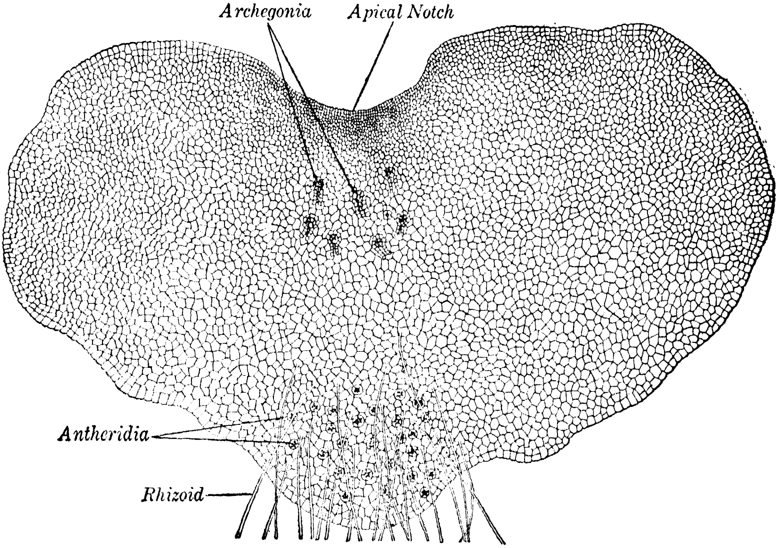


FIG. 292. Mature fern prothallium viewed from below.

rarely observed in nature unless sought for. Fully grown prothallia are often not more than a quarter inch in diameter.

The prothallium is the sexual generation or gametophyte of a fern, and like the gametophyte of a moss it produces gametes. In

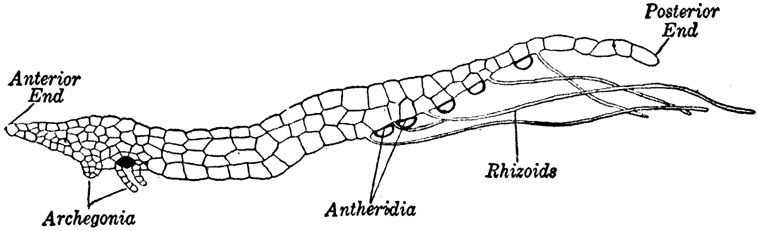


FIG. 293. Vertical lengthwise section of a fern prothallium.

some species of mosses, gametes of both kinds are borne by the same gametophyte; in other species, antherozoids and eggs are borne on separate plants. The bracken is like the mosses of the former type, in that antherozoids and eggs may be produced by the same gametophyte. If prothallia are small and poorly nour-

ished, they often form only antheridia and antherozoids, but such prothallia may develop archegonia and eggs if they are placed under better conditions for food-making. Antheridia may occur on almost any part of the plant but are most numerous on the under surface, particularly on the posterior portion of the pro-

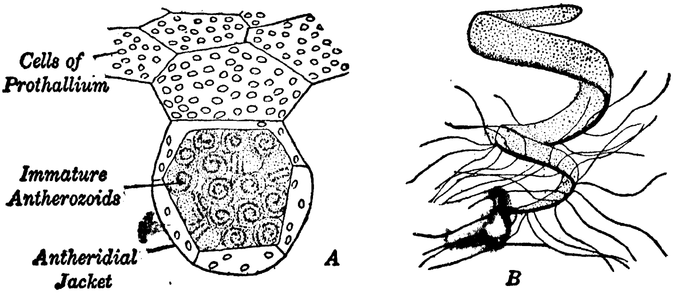


FIG. 294. *A*, antheridium of a fern. *B*, antherozoid.

thallium, where rhizoids are abundant. Archegonia are borne also on the under surface, but only on the cushion of cells back of the apical notch.

An antheridium (Fig. 294, *A*) is dome-shaped and much smaller than an antheridium of a moss. The few cells of its outer layer

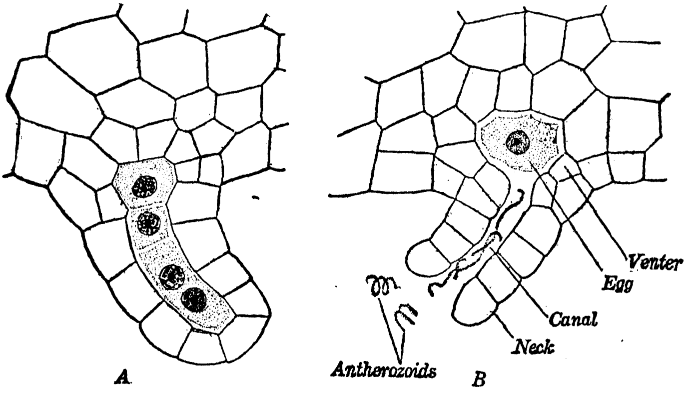


FIG. 295. *A*, nearly mature archegonium of a fern. *B*, archegonium at the time of the entrance of antherozoids.

constitute a jacket. After a series of cell divisions, each interior cell develops into an antherozoid (Fig. 294, *B*) which is larger than the antherozoid of a moss and has the form of a short spiral. Borne

on its slender anterior portion are many flagella by means of which the antherozoid swims rapidly.

An archegonium (Fig. 295) has essentially the same structure as an archegonium of a moss, but is smaller and composed of fewer cells. Its venter is imbedded in the cushion of the prothallium. Its neck is short and usually curves backward from the notch toward the older portion of the prothallium. At maturity, the cells of the canal row disintegrate and the cap cells of the neck break apart, leaving a passage-way to the egg. Although sex organs

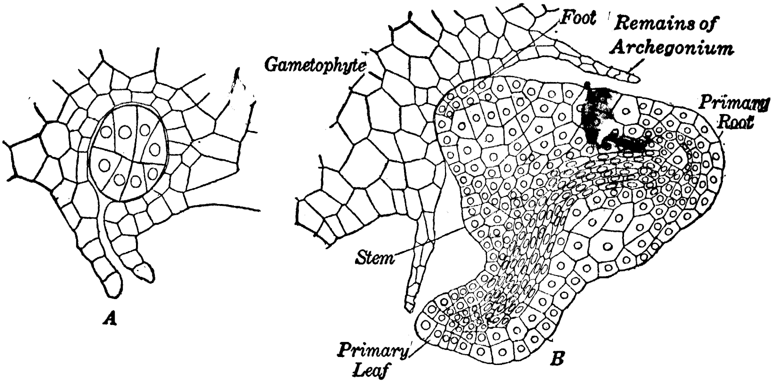


FIG. 296. *A*, early stage in the development of a fern embryo within the venter of an archegonium. *B*, an embryo, still partly within the archegonium, differentiated into foot, primary root, primary leaf, and stem.

of both kinds are produced on the same prothallium, most of the antheridia usually develop and discharge their antherozoids before the archegonia on the same plant have matured. Hence the union of gametes from different plants, rather than from the same plant, is probably the rule in the bracken. Such union is made possible by the fact that the prothallia grow in groups in moist places.

284. Development of an Embryo (Fig. 296). Though many antherozoids may reach the mouth of an archegonium and enter the neck, only one unites with the egg. The zygote, like that of a moss, germinates within the venter of the archegonium. After a few divisions, forming a small mass of cells, the young sporophyte (*embryo*) becomes four-lobed. By further division and growth, one lobe develops into a *foot*, a small organ imbedded in the prothallial cushion; from this cushion the foot absorbs food for the embryo. Another lobe develops into a *primary root*, which

pushes downward through the surrounding tissues and grows into the soil. A third lobe gives rise to a *primary leaf* which, growing outward and forward beneath the prothallium, turns upward at the notch and develops a green blade much simpler in form than the blades of the leaves to be produced later. The *stem* develops slowly from the fourth lobe. Until the time of the production of the primary root and primary leaf, the embryo (young sporophyte) has been parasitic upon the gametophyte (Fig. 297). With the full development of the primary leaf and primary root, however, the sporophyte becomes an independent plant, and somewhat later the gametophyte dies. The stem grows slowly into the soil, producing secondary leaves and secondary roots. After the formation of several secondary leaves and secondary roots, the primary leaf and the primary root die. Thus the mature sporophyte has been derived from only one lobe of the embryo, namely, that which developed into the stem.

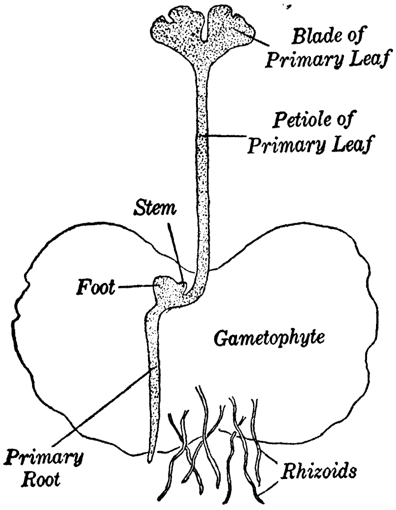


FIG. 297. Young sporophyte still attached to, and parasitic upon, the gametophyte.

285. Life Cycle (Fig. 298). The life cycle of the bracken, like that of a moss, includes two distinct phases. A spore gives rise to a minute green plant, the gametophyte, which forms sex organs bearing gametes. The union of gametes (antherozoid and egg) forms a zygote, which on germination produces an embryo parasitic upon the gametophyte. By further growth the embryo develops into a large, independent plant, the sporophyte, consisting of stem, roots, and leaves. On some of the leaves are borne sporangia which contain spores, completing the cycle.

While the histories of moss and fern are alike in general outline, there are important differences. The gametophyte of a moss is relatively large and may live for a number of years, whereas its sporophyte is relatively small and short-lived. In a fern the game-

tophyte is very small and comparatively short-lived, while the sporophyte is large and may live for many years. The conspicuous moss plant is the gametophyte; the conspicuous fern plant is the sporophyte.

Other Ferns

286. Leaves. Although all ferns are alike in the general characteristics that indicate their relatively close relationship, different

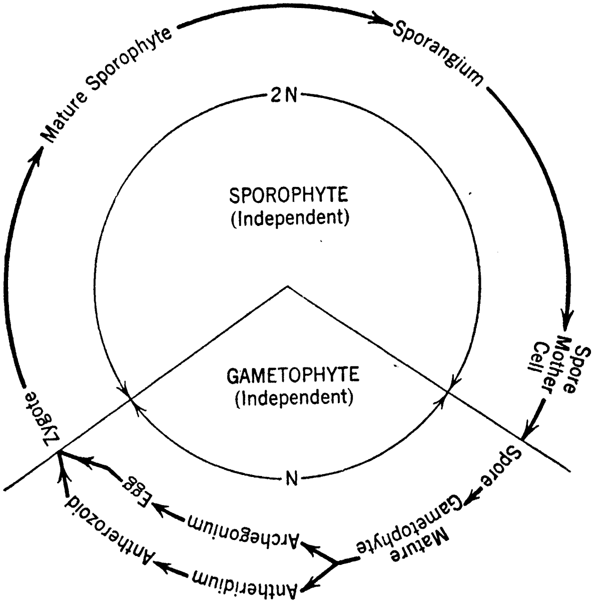


FIG. 298. Life cycle of a fern.

species vary markedly in form and structure. The differences are evident chiefly in the sporophytic generation. The gametophytes of most ferns are essentially like the gametophyte of the bracken.

One conspicuous feature in which ferns differ from one another is in the form of the leaf blade. The "walking fern" represents a type whose blades are not lobed or divided. A leaf blade of this fern has the shape of a greatly elongated triangle whose slender tip grows until it bends over and comes into contact with the soil. When the tip touches the soil it develops a small bud that gives rise to roots and a stem, and so produces a new plant. A repetition

of this process by the successively formed new plants explains the name given this fern. Some ferns, such as the common polypody, have simple but very deeply lobed leaf blades. Others, including the royal fern, the lady fern, and the male fern, produce pinnately divided leaves, each primary leaflet being also pinnately lobed or divided. The petiole of the maidenhair fern is forked at the summit, each of the two divisions so formed bearing on one side several spreading, pinnately divided leaflets.

287. Sporangia. The sporangia of most ferns, unlike those of the bracken, are produced in rounded or linear groups (*sori*) on the

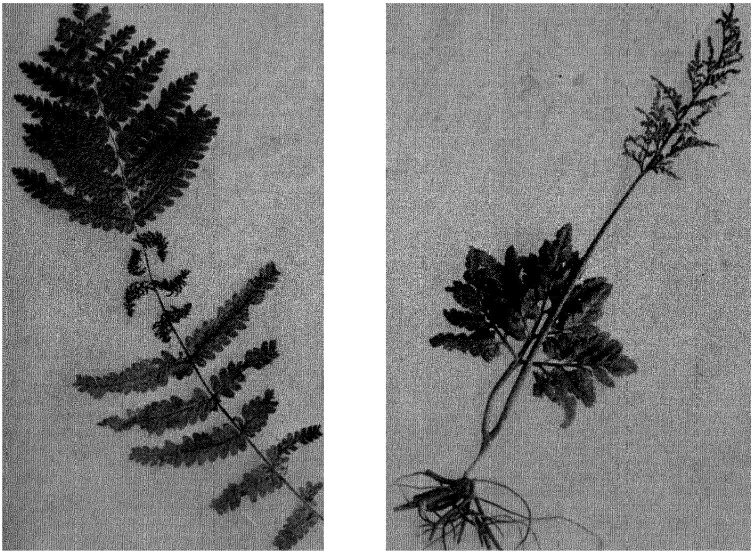


FIG. 299. Left, the interrupted fern. Right, the grape fern.

under surfaces of leaf blades. Each sorus is borne upon an elevated cushion of tissue, and in some ferns is covered by a variously shaped outgrowth of the leaf.

In the bracken, as has been seen, many leaves bear sporangia—that is, are sporophylls; those leaves which are sterile otherwise resemble the sporophylls. In the interrupted fern (Fig. 299) the production of sporangia is confined to several pairs of leaflets near the middle of the blade. These leaflets are small and brown, and on their margins are borne numerous sporangia; the other (sterile)

leaflets are larger and green. After the spores are shed in the early summer the spore-bearing leaflets wither. The sporangia of the royal fern are borne on a few leaflets at the apex of the leaf blade. A leaf of the grape fern (Fig. 299) consists of two distinct parts: one is a flat, much-divided blade which performs most of the photosynthetic work; the other part of the leaf has as its function only the production of spores. In a few species, including the cinnamon fern, the sensitive fern (Fig. 300), and the ostrich fern, there are two different kinds of leaves. Those of one sort, the sterile leaves, are broad and green and are photosynthetic organs; those of the

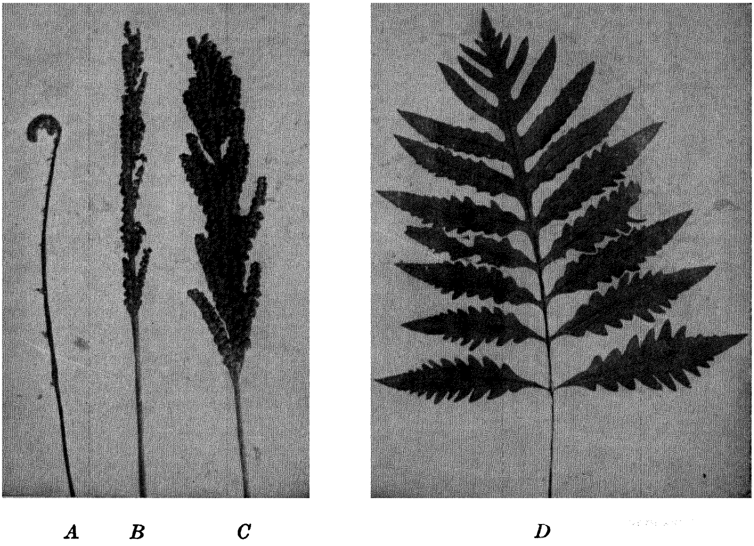


FIG. 300. Fertile (*A–C*) and sterile (*D*) leaves of the sensitive fern.

other sort, the sporophylls, are brown at maturity and function only in spore-production.

288. Roots (Fig. 301). The roots of all ferns are essentially similar in the structure and arrangement of their tissues. In the mature region of a root a relatively thick cortex encloses a small central stele. On its outer side the cortex is bounded by an epidermis one cell in thickness. The cortical cells are for the most part thin-walled and often contain numerous starch grains. The cells of the endodermis are distinguished by thickenings on their radial walls. Next within the endodermis is the pericycle, consisting of

one or two layers of thin-walled cells. At various points just within the pericycle are strands of xylem separated from one another (in a young portion of the mature region) by thin-walled cells. While the first-maturing portions of these xylem strands, consisting of small cells, are adjacent to the pericycle, the later-maturing portions extend the strands inward toward the center of the stele so that in most cases a central solid mass of xylem is eventually formed. Just within the pericycle and alternating with

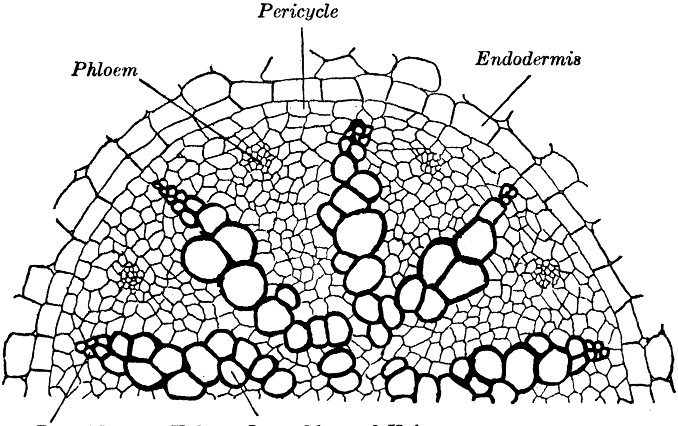


FIG. 301. Cross section of a portion of the stele and cortex in a root of Angiopteris.

the first-maturing strands of xylem are small strands of phloem. Such a stele, in which the xylem forms a more or less solid central column with the phloem on its outer side, is a *protostele*.

The arrangement of xylem just described is an *exarch* arrangement. Exarch xylem is characterized by the fact that the first-matured xylem elements are at the outer margin of the stele adjacent to the pericycle, the later-maturing xylem elements lying inward from those first matured. A protostele with such a xylem-arrangement is an *exarch protostele*. All roots, both in pteridophytes and in seed plants, have exarch steles; in many cases these are protosteles; but in others, the center of the root is occupied by pith.

289. Stems. The stems of ferns, unlike their roots, vary greatly in external form and in internal structure. Many ferns growing in temperate regions, like the bracken, have underground stems. In the tropics, however, there is greater diversity. Here some

species grow perched on the limbs and branches of trees. The stems of other species are prostrate on the ground or clamber upon other plants. Still other species have stems beneath the soil. In the tropics also are found tree ferns (Fig. 285).

An exarch protostele seems to represent the most primitive type from which all other types of stele have been derived. As has been seen, the primitive exarch protostele is still characteristic of roots; in the stems of most pteridophytes and seed plants, however, other stelar types derived from the exarch protostele are found. The stems of only a few ferns have protosteles; one of these is *Gleichenia flabellata,* which grows chiefly in the tropics and subtropics. The stem of Gleichenia has a thick-walled epidermis, beneath which is a cortex some of whose cells have relatively thick walls. A single-layered endodermis encloses the pericycle, which may be several cells in thickness. Within the pericycle is a thin cylinder of phloem; and entirely enclosed by the phloem is the xylem which fills the center of the stele. A few parenchymatous cells are scattered through the xylem. This protostele differs from that of a root in the course of development of its xylem. The first xylem elements to mature are, as in a root, groups of small cells developing at various points within the pericycle. However, the later-maturing xylem not only develops to the center of the stele but also surrounds the first-matured strands. This arrangement, in which the later-maturing xylem surrounds the first-matured strands, is a *mesarch* arrangement. Whereas the root of a fern contains an exarch protostele, the stem of Gleichenia has a *mesarch protostele.*

The maidenhair fern (*Adiantum pedatum*) illustrates a still more advanced type of stem structure. Its stele encloses a central pith. In the stele, midway between pith and cortex, is a continuous cylinder of xylem. On both inner and outer faces of the xylem are, successively, phloem, pericycle, and endodermis. This type of cylindrical stele with a central pith is a *siphonostele.* The siphonostele of Adiantum has both internal and external phloem; in most siphonosteles, however, phloem is present only on the outer side of the xylem.

The xylem of Adiantum, like that of Gleichenia, is mesarch. Adiantum, therefore, has a *mesarch siphonostele.* Just as the mesarch condition has been derived from the exarch, so an *endarch* condition, in which the first-matured xylem elements are on the

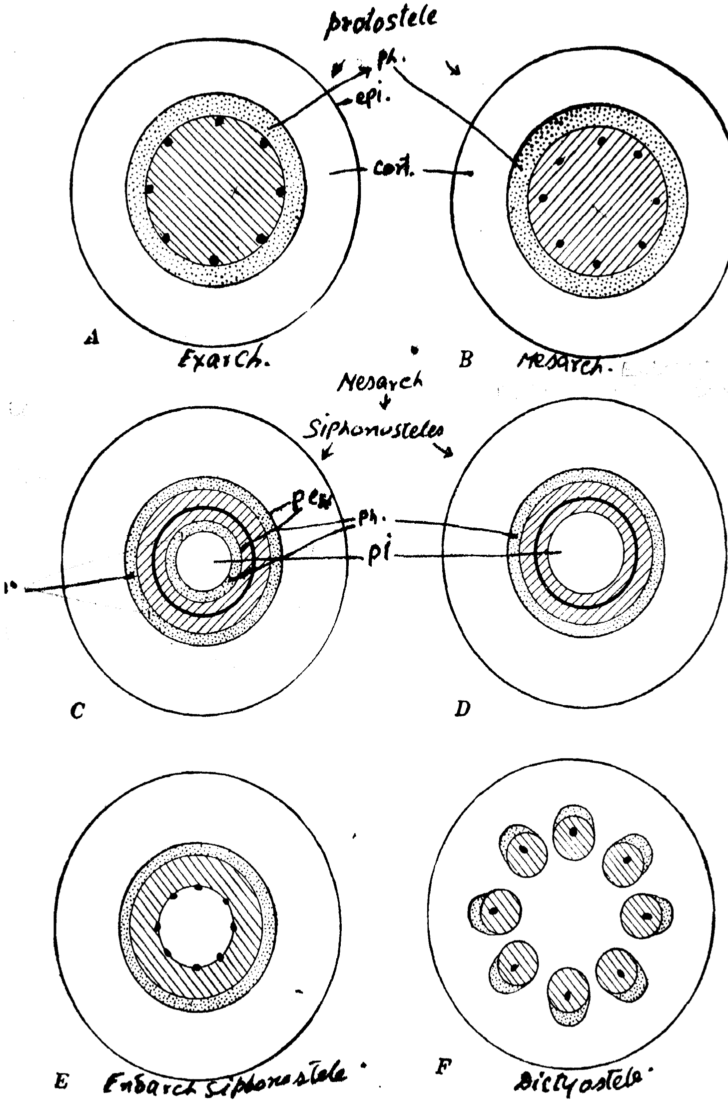


FIG. 302. Diagrams of various types of fern steles; the first-matured xylem in all cases is in black, the later-matured xylem diagonally shaded, the phloem stippled; pith and cortex are unshaded. *A*, exarch protostele. *B*, mesarch protostele. *C*, *D*, mesarch siphonosteles with (*C*) phloem on both sides, and (*D*) on the outer side only, of the xylem. *E*, endarch siphonostele. *F*, dictyostele.

inner face of the xylem zone, has been derived from the mesarch. The endarch condition is characteristic of the stems of nearly all living seed plants.

As a young leaf of Adiantum grows and develops, a vascular strand is formed, extending outward from the stele through the cortex of the stem and into the petiole. Beyond the junction of leaf trace and stele there is in the stele of the stem a long, slender area in which parenchymatous cells are formed instead of xylem and phloem. This elongated interruption of the stele just ahead of the junction of each leaf trace, in which only parenchymatous cells are formed, is a *leaf gap*. In many ferns leaf gaps are long and numerous, giving to the stelar cylinder the form of a network of bundles with elongated meshes. In cross section such a network has the appearance of separate bundles arranged in a circle about a central pith. This type of stele is a *dictyostele*. Such a stele occurs in the stem of Polypodium. The arrangement of bundles in the stem of the bracken represents a modified type of dictyostele.

290. Bryophytes and Ferns. About 150 genera and more than 6,000 species of ferns are known. They constitute a class standing conspicuously higher than the bryophytes in the sense that they have advanced further from a primitive condition. Like the bryophytes the ferns have a distinct alternation of generations. The sporophyte of a bryophyte is small, relatively simple, and always attached to and largely dependent upon the gametophyte. The sporophyte of a fern, on the other hand, is a relatively large, complex plant differentiated into stem, leaves, and roots, and therefore independent of the gametophyte. The fern gametophyte, however, does not show a corresponding development. Although an independent green plant, it is always very small and simple in structure. In spite of the radical change in relative size and complexity whereby the sporophyte has become the large, conspicuous generation, the gametophyte still retains the function of producing gametes and the sporophyte continues to produce spores.

CHAPTER XXVII

SOME OTHER PTERIDOPHYTES

Equisetum

291. Nature. The few living species of *Equisetum* ("horsetails") are related to a group of plants which, during one period of the earth's history, formed a conspicuous feature of its vegetation. Some of these ancient plants developed into good-sized trees, but the present-day species of Equisetum are mostly small. In tropical South America, the stems of one species grow to a height of more than 30 feet. Its stems are, however, very slender and lean upon the shrubs and trees among which they grow.

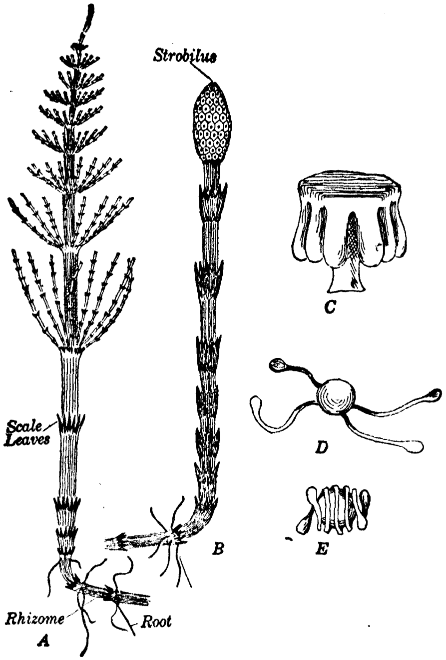


Fig. 303. Sporophyte of Equisetum. *A*, sterile aërial branch. *B*, fertilé aërial branch. *C*, sporophyll. *D*, *E*, spores with spiral bands uncoiled (*D*) and coiled (*E*).

Equisetum is almost world-wide in its distribution and thrives in a variety of habitats. Certain species grow in ponds and in swamps; others in meadows and in damp, shaded places; and still others in relatively dry and exposed situations such as sandy embankments.

292. Sporophyte. *Equisetum arvense* (Fig. 303) is common in habitats of the type last mentioned. The sporophyte of this species is composed of a horizontal, branching underground stem and of aërial branches, some sterile and some fertile, which grow upward from the nodes of the stem. The underground stem

when dry and coiling about the spore when moist. The bands of several spores may become entangled; the spores, therefore, are shed in small clusters and may germinate to form groups of gametophytes.

294. Gametophyte and Embryo. The germination of a spore results, as in a fern, in the formation of a small green prothallium (Fig. 305) which bears sex organs. A prothallium of Equisetum differs from that of a fern in its form and in the location of the sex organs. When mature, it is usually a disk-shaped cushion several cells in thickness, from whose upper surface arise irregularly lobed, flattened branches each one cell thick. Rhizoids grow from the lower surface of the cushion. Antheridia are borne usually near the apices of the vertical branches; archegonia, on the upper surface of the cushion at the bases of the branches. An antherozoid resembles one of a fern in having many flagella.

An embryo in its early stages of development is in most respects similar to that of a fern. Lobes of a young embryo develop respectively into a foot, a primary stem bearing two to four primary leaves, and a primary root. The primary stem remains very small. At its base a bud arises that grows into a larger branch. In like manner at the base of this first branch a second branch arises, and the process may be repeated. Eventually one of the later-formed branches grows downward, penetrates the soil, and develops into the characteristic stem from which sterile and fertile aërial branches subsequently arise.

Club Mosses: Lycopodium

295. Sporophyte. The club mosses also are related to an old group of plants once very abundant. Some of the ancient club mosses were tree-like. The present-day members of the group are all small. The plants familiarly known as "club mosses," "ground pines," and "Christmas greens" are members of the genus *Lycopodium* (Fig. 306). The various species of this genus occur in tropical as well as in temperate regions. Some tropical and subtropical species grow on trunks and branches of trees. Those of temperate regions grow on the ground. The form of the sporophyte differs somewhat according to the species. Often it has a branching stem which creeps over the surface of the ground or lives within the soil, producing slender roots and sending up aërial branches. The aërial stems and branches are usually well covered with small,

narrowly triangular, sessile leaves. The leaves are relatively simple in structure, being only a few cells in thickness. Stomata are present; the internal cells of a leaf are all similar excepting those of the phloem and xylem, which compose an unbranched vein or midrib extending from the base of the leaf part-way toward the apex. The stem has an epidermis, a thick cortex, and a stele. The xylem and phloem of the stele are in plates whose arrangement varies with the species as well as with the direction of growth of the stem.

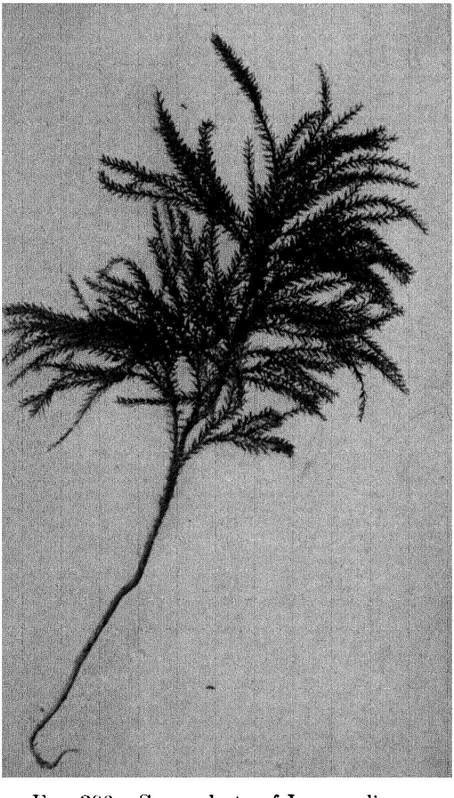


FIG. 306. Sporophyte of Lycopodium.

296. Spore-formation. On the inner side, and near the base, of each of certain leaves is a small sporangium (Fig. 307, *C*). Such leaves are *sporophylls*. In some species of Lycopodium, the sporophylls are not readily distinguishable, either by their appearance or by their position, from the sterile (foliage) leaves. In other species the sporophylls are borne, more or less compactly grouped, on the terminal portions of some of the upright branches, which thus constitute *strobili* (Fig. 307, *A*, *B*). In such a case the sporophylls are smaller, and contain a lesser proportion of chlorophyll, than the foliage leaves. Each sporangium has a short stalk, and a jacket several cells in thickness. Within the sporangium are developed many spore mother cells, each of which finally divides to form four spores.

297. Gametophyte and Embryo. The spores seem to lie dormant for several years after being shed. In the majority of species, a spore on germination forms a small subterranean, saprophytic gametophyte (Fig. 308), on whose upper portion are borne antheridia and archegonia. In general plan the sex organs resemble those

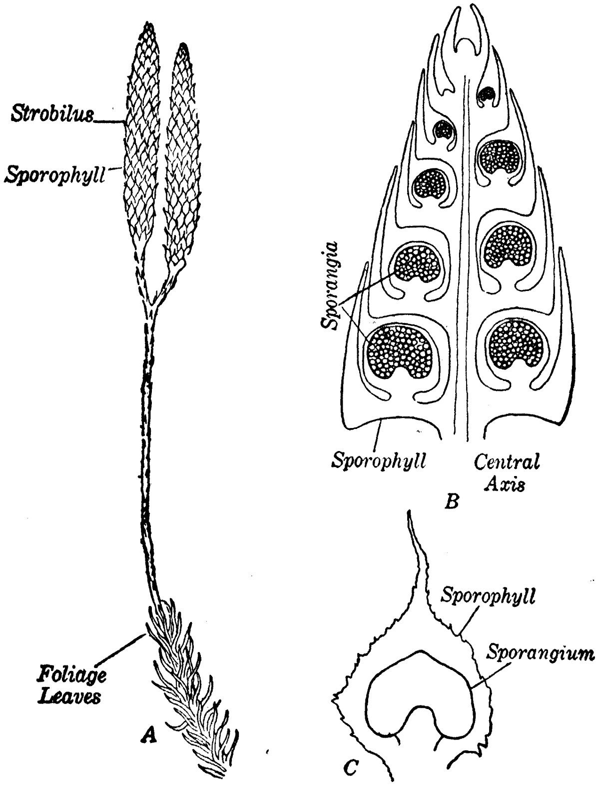


FIG. 307. Lycopodium. *A*, branch bearing 2 strobili. *B*, lengthwise section of the tip of a strobilus (diagrammatic). *C*, sporophyll bearing a sporangium.

of a fern, differing, however, in the fact that they are more or less imbedded in the gametophyte. An antherozoid, unlike one of a fern or of Equisetum, has two flagella, resembling in this respect the antherozoids of liverworts and mosses.

The zygote divides by a transverse wall into an outer and an inner cell. The outer cell ordinarily elongates, becoming a *sus-*

pensor. The inner cell, which has been pushed by the elongation of the suspensor deeper into the tissue of the gametophyte, develops into an embryo. The suspensor is therefore only a temporary organ which functions in bringing the embryo into a better nutritive relation. The embryo is at first dependent upon the gametophyte, securing its food by means of a foot. Later, by the growth of stem and leaves above the soil, and by the development of a first root under the soil, the embryo becomes an independent plant.

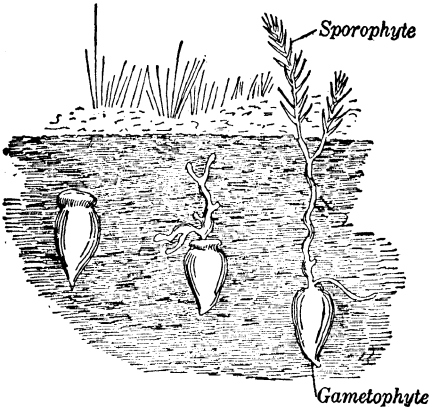


FIG. 308. Underground gametophytes of Lycopodium, the 2 at the right bearing sporophytes.

The Smaller Club Moss, Selaginella

298. Sporophyte. The members of this genus are mostly tropical plants, although a few grow in temperate regions. Some species of temperate regions live on rocks and on dry, sandy soil; others thrive best in more moist and shaded habitats.

The conspicuous plant, as in the case of a fern, is the sporophyte (Fig. 309). Its branching stem bears many small, simple leaves. The stem, in some species, grows along the ground and bears two rows of small leaves and two rows of larger leaves. In other species the branches of the stem grow more or less upright, and the leaves are uniform in size. Roots develop directly from the stem in certain species; in others, they arise from short, leafless branches.

In some species the stem contains a small, centrally placed stele. The xylem of the stele is surrounded successively by phloem, pericycle, and endodermis, the latter in many species being peculiar in that it is interrupted by large intercellular spaces. The inner part of the cortex is commonly composed of thin-walled cells, but the cells of the outer portion are usually thick-walled. An epidermis encloses the cortex.

The leaves are small, unlobed and undivided, narrowly triangular, and pointed. A leaf has an upper and a lower epidermis,

between which is spongy tissue containing a single vascular bundle or midrib. Stomata occur chiefly in the lower epidermis.

299. Spore-formation. The leaves on the terminal portions of many of the branches are more or less compactly arranged in four rows. At the inner side of each of these leaves, near its base (Fig. 310), is a small, short-stalked sporangium. A leaf that bears a sporangium is a *sporophyll,* and the limited portion of a branch which bears sporophylls, together with the sporophylls themselves, is a *strobilus.* The sporangia borne on different sporophylls in the same strobilus are of two distinct kinds (Figs. 311, *A;* 312, *A*). Each sporangium of one kind contains commonly four relatively large spores; sporangia of the other kind contain many very small spores. The large spores are *macrospores,* the sporangium which contains them is a *macrosporangium,* and the leaf on which this sporangium is borne is a *macrosporophyll.* In like manner, the small spores are *microspores,* the sporangium which contains them is a *microsporangium,* and the leaf on which this sporangium is borne is a *microsporophyll.* The distribution of micro- and macrosporophylls upon the axis of the strobilus differs in different species; in some species (Fig. 310), the lower sporophylls are macrosporophylls, the upper are microsporophylls; in others, one side of the strobilus bears microsporophylls, the other side macrosporophylls; in still other species, the two types of sporangia are intermingled.

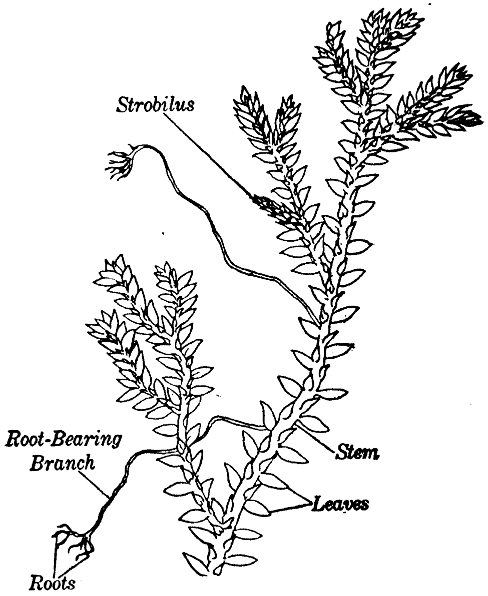


FIG. 309. Portion of a mature sporophyte of Selaginella.

A mature sporangium of either type has a short stalk and a jacket three cells in thickness. A macrosporangium is larger than a microsporangium and is generally lobed, the lobes corresponding

to the positions of the macrospores within. Both macro- and microsporangia develop alike to the spore-mother-cell stage. In some sporangia, most of the numerous spore mother cells divide to form four spores each. The result is the production of a large number of small spores (microspores) in such a sporangium. In other sporangia, usually all but one of the spore mother cells disintegrate. From this remaining spore mother cell, by two successive divisions, four spores (macrospores) are formed, some or all of which increase greatly in size and develop thick, corrugated walls.

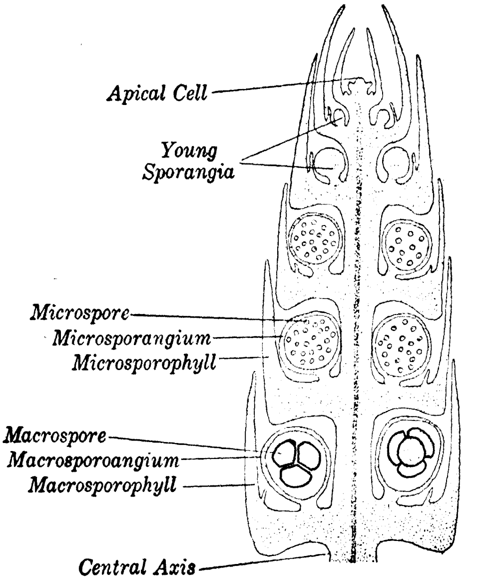


FIG. 310. Diagram of a lengthwise section of a portion of a strobilus of Selaginella.

The difference in size between the two kinds of spores is associated with a difference in their function. A macrospore develops into a *macrogametophyte* (female gametophyte); a microspore into a *microgametophyte* (male gametophyte).

300. Macrogametophyte (Fig. 311, *B*). A macrospore has somewhat the shape of a low, broad pyramid with a rounded base. It possesses a single nucleus. While held closely within the macrosporangium, the macrospore develops into a macrogametophyte. Its development begins with a series of nuclear divisions, not immediately followed by cell divisions. The free nuclei are more or less evenly distributed in the dense cytoplasm lining the inner surface of the spore wall. After a number of nuclear divisions, cell divisions occur between those nuclei lying near the pointed end of the macrospore wall. The cells so formed may undergo further growth and division, and on the cushion of cells thus produced archegonia develop.

In many species of Selaginella, at some stage in the development

of the macrogametophytes as described above, the macrosporangia mature and break open and the macrogametophytes fall to the ground. If conditions are favorable, macrogametophyte-development continues. At about the time that archegonia are being formed, the wall of each macrospore cracks open at its pointed end, exposing the slightly protruding portion of the macrogame-

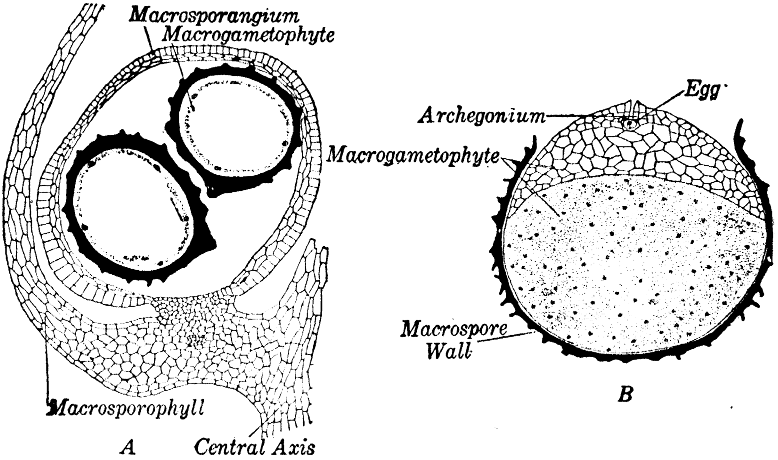


FIG. 311. Selaginella. *A*, section through a macrosporangium. *B*, macrogametophyte; redrawn from Miss Lyon.

tophyte, which bears archegonia. The partly imbedded archegonia resemble those of the bracken but are fewer-celled. Although the protruding portion of the macrogametophyte may develop chlorophyll, the macrogametophyte depends chiefly upon stored food supplied during its development by the sporophyte.

301. Microgametophyte. A microspore (Fig. 312, *B*), except for its much smaller size, closely resembles a macrospore in shape and structure. It germinates (Fig. 312, *C–E*) while still within the microsporangium. Its division results in the formation of a large and a small cell, both of which are wholly within the microspore wall. The smaller is the *prothallial cell,* so called because this single cell is thought to correspond to the vegetative tissue of a fern prothallium. From the larger cell, by further divisions, is developed a central group of cells surrounded by a single layer of jacket cells. Each cell of the central group is finally transformed into a spirally coiled antherozoid with two flagella, the jacket cells meanwhile having disintegrated.

In many species of Selaginella, the microsporangia at maturity break open and the gametophytes at some stage in their development fall to the ground. Here their further development continues. After antherozoids have been formed, the layers of the spore wall break open and the antherozoids are liberated. If the micro- and

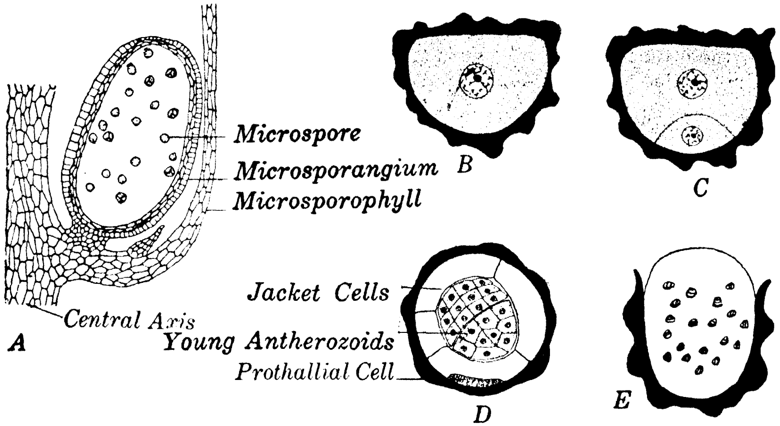


FIG. 312. Selaginella. *A*, section through a microsporangium. *B*, microspore. *C*, microgametophyte after the formation of the prothallial cell. *D*, nearly mature microgametophyte. *E*, mature microgametophyte with antherozoids. *B–E* redrawn from Miss Lyon.

macrogametophytes lie near together on the ground, a film of water connecting them will enable the antherozoids to swim to the archegonia. As in mosses and ferns, one antherozoid unites with each egg.

302. Embryo (Fig. 313, *A*). Shortly after gametic union, cell divisions occur in the previously undivided basal portion of the macrogametophyte. The zygote divides into two cells. The daughter cell nearer the neck of the archegonium elongates, forming a *suspensor* that pushes the other daughter cell farther into the tissue of the macrogametophyte. The latter daughter cell develops into an embryo, consisting of a foot, a stem bearing two primary leaves, and a primary root. The primary root and the stem bearing the primary leaves grow outward from the tissue of the macrogametophyte, and the young sporophyte becomes independent (Fig. 313, *B*). As the stem continues its growth, it develops secondary leaves and secondary roots; the primary root and primary leaves eventually disappear.

Although the history of the gametophytes recited above is characteristic of many species of Selaginella, a modification of the story is found in certain species. This latter account is of interest because these particular species closely approach the seed habit characteristic of spermatophytes. In these species, macrogametophytes develop in the manner already described. When a macrosporangium is mature it cracks open, but not sufficiently to permit

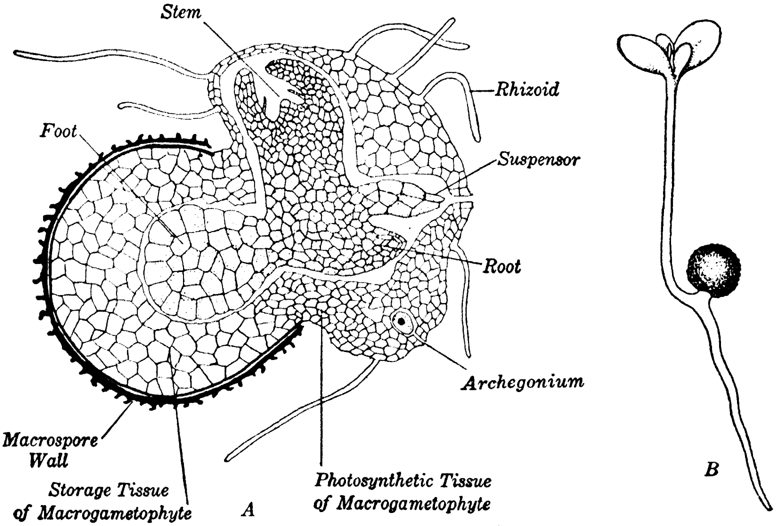


FIG. 313. Selaginella. *A*, macrogametophyte with a young sporophyte; redrawn from Bergen and Davis. *B*, macrogametophyte with an older sporophyte which is still parasitic upon the gametophyte.

the escape of the developing macrogametophytes. The microsporangia, however, when mature burst open and the developing gametophytes are thrown out. Some of them, sifting down between the sporophylls, fall by chance into the partly opened macrosporangia. Lying now in the same sporangium, the two kinds of gametophytes complete their development. If sufficient water is present, gametic union occurs. At some time later, the opening of the macrosporangium becomes larger and the macrogametophytes with the developing embryos may fall to the ground.

303. Life Cycle (Fig. 314). A strobilus produces two kinds of sporophylls, two kinds of sporangia, and two kinds of spores. A macrospore develops into a macrogametophyte which forms arche-

gonia. Each archegonium contains an egg. A microspore develops into a microgametophyte which produces antherozoids. The union of antherozoid with egg forms a zygote. The zygote grows into an embryo parasitic on the macrogametophyte. By further growth and development the embryo becomes a mature sporophyte—an

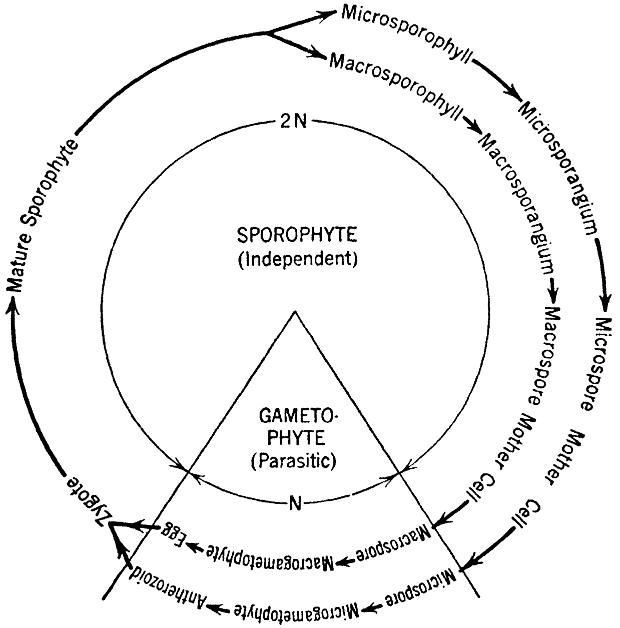


FIG. 314. Life cycle of Selaginella.

independent plant composed of stem, roots, and leaves and bearing strobili.

As in a moss or fern, the chromosome number is doubled in gametic union; it is reduced in the two successive divisions by which four macrospores are formed from a macrospore mother cell, and likewise in the divisions by which four microspores are formed from each microspore mother cell. In Selaginella, therefore, as in mosses and ferns, the gametophytic generation (here including macrogametophyte and microgametophyte) is marked by the presence in each of its cells of n chromosomes; and the sporophytic generation by the presence in each of its cells of $2n$ chromosomes.

304. New Features in Selaginella. From an evolutionary standpoint, Selaginella shows certain marked advances over the ferns.

One notable advance in Selaginella is in the production of two kinds of spores, each of which develops into a specific kind of gametophyte. A microgametophyte is a greatly reduced plant in that it consists of relatively few cells. In the same sense, a macrogametophyte also is greatly reduced as compared with the gametophyte (prothallium) of a fern. A microgametophyte develops to maturity within the wall of the microspore; a macrogametophyte develops chiefly within the wall of the macrospore and barely protrudes from this wall when mature. The male (micro-) and female (macro-) gametophytes are markedly different. But in Selaginella sexual differentiation is not limited to the gametophyte, as it is in bryophytes and ferns. Instead, this differentiation has been pushed back, as it were, to the sporangia, which are structures belonging to the sporophyte. Hence the difference between the sporangia, although these are strictly asexual reproductive structures, is nevertheless actually a sexual difference.

Another important difference concerns the nutrition of the gametophytes. A microgametophyte, having no chlorophyll, is entirely dependent upon foods received from the sporophyte. That is, it has become indirectly parasitic upon the sporophyte. A macrogametophyte also is chiefly dependent upon foods derived from the sporophyte; although, in its later development, that part of a macrogametophyte which is exposed by the cracking of the macrospore wall may develop chlorophyll and carry on a very limited amount of photosynthesis. Thus the nutritive relationships which existed between gametophyte and sporophyte in the mosses and liverworts have been virtually reversed in Selaginella. In a moss or liverwort, the sporophyte is largely parasitic upon the gametophyte. In Selaginella, the gametophytes have become in effect parasitic upon the sporophyte.

A third important characteristic of certain species of Selaginella is that a young microgametophyte, on being discharged from its sporangium, may sift into a partly open macrosporangium and there, in close proximity to a developing macrogametophyte, continue its development.

A fourth new feature in the species just referred to is that the macrogametophyte, surrounded largely by the macrospore wall, may remain within the partly open macrosporangium during gametic union and the early stages of embryo-development. Hence these species of Selaginella approach closely the formation of a

seed, the production of which is one of the outstanding features of the seed plants.

305. Pteridophytes. The ferns and their allies constitute a division, *pteridophytes*, whose members are approximately at a common level of development in the sense that they stand higher in the evolutionary scale than do bryophytes, but have not attained the seed habit characteristic of spermatophytes.

In general, the sporophyte of a pteridophyte is a relatively large, independent plant differentiated into stem, leaves, and roots. Sporangia are usually borne on leaves. The sporophylls are therefore an important feature. In some pteridophytes the sporophylls bear sporangia in which the spores are all alike; in others there are two sorts of sporophylls, of sporangia, and of spores. In certain pteridophytes sporophylls are grouped together, forming cones (strobili).

The gametophytes of pteridophytes, always small, are variable from genus to genus, both in structure and in method of nutrition. Some gametophytes, such as those of most ferns and of Equisetum, are green, independent prothallia; others, including those of Lycopodium, grow underground and are saprophytic.

Those pteridophytes with two sorts of spores form simpler gametophytes which, developing almost entirely within the old spore walls, are extremely small and indirectly parasitic upon the old sporophytes. The antherozoids, however, are motile, and the presence of water is still essential to gametic union. A sporophyte begins its existence as a parasite, but eventually, through the production of stem, roots, and leaves, becomes an independent plant.

CHAPTER XXVIII

GYMNOSPERMS

306. Seed Plants. The spermatophytes or seed plants constitute the highest division of the plant kingdom. In this division the sporophyte reaches its greatest complexity; the gametophytes are reduced to minute plants parasitic upon the sporophyte. Seed plants are divided into *gymnosperms*, whose seeds are not enclosed, and *angiosperms*, which have enclosed seeds.

The geological record shows that during certain periods of the earth's history gymnosperms were relatively abundant; indeed, some orders are known only in the form of fossils, and one order is now represented by but a single surviving species. The largest orders of living gymnosperms are the *Cycadales* and the *Coniferales*. Cycadales are all tropical or subtropical; Coniferales, which include the pines, spruces, and related trees and shrubs, are mainly inhabitants of temperate regions.

ZAMIA

307. Sporophyte. The Cycadales are the most primitive of living seed plants and in certain respects show greater similarities to pteridophytes than do any other existing seed plants. *Zamia* (Fig. 315), a member of this order, grows extensively in Florida. The sporophyte, which is the conspicuous generation, rarely attains a height of more than four feet. Its stem is short, thick, and erect, frequently with its greater portion underground. At its center (Fig. 316) is a large pith, surrounded when the stem is young by a cylinder of vascular bundles. Each bundle consists, like a bundle of a dicotyledonous stem, of xylem, cambium, and phloem. As the stem grows older, only small amounts of secondary xylem and secondary phloem are formed by the activity of the cambium. The xylem so formed is not differentiated into annual rings; it is interrupted by relatively wide medullary rays. In the thick cortex great amounts of starch are stored, the quantity being so large that the plant was used as a source of food by the Seminole Indians under the name of "conti."

The foliage leaves arise in a crown near the apex of the stem, a cluster of new leaves being produced from year to year. The leaves are leathery in texture and resemble those of many ferns in being pinnately divided. The tip of each young leaf unrolls slightly, in this respect somewhat resembling a fern leaf. The individual leaflets, however, do not unroll, as is the case in a pinnately divided fern leaf. A leaf of Zamia may live for several years. As the older leaves die and wither, their bases remain attached for a short time to the stem.

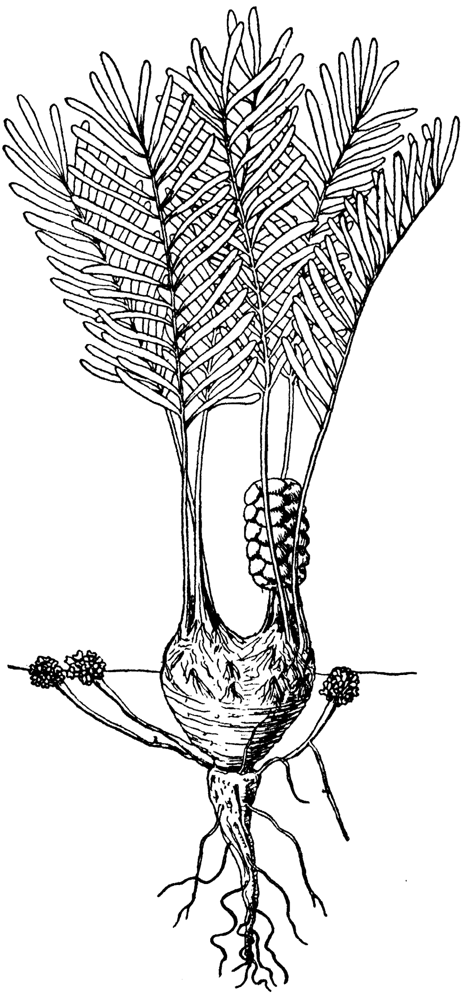


FIG. 315. Mature sporophyte of Zamia bearing a carpellate strobilus.

Zamia usually forms a relatively large tap root from which a few slender branching roots arise. A blue-green alga gains entrance into the cortex of some of the smaller roots; the stimulus resulting from its presence causes each invaded root to change its direction of growth and to produce a compact cluster of small tubercular branch roots at or near the surface of the soil.

A tap root or one of the larger branch roots commonly possesses a siphonostele. The exarch primary xylem and the primary phloem alternate in the radial arrangement characteristic of roots. Secondary xylem and phloem are formed by cambial activity.

In the younger portions of a tap root the cortex is relatively thick and stores abundant foods. In older portions a cork cambium is formed in the pericycle. After this cork cambium has

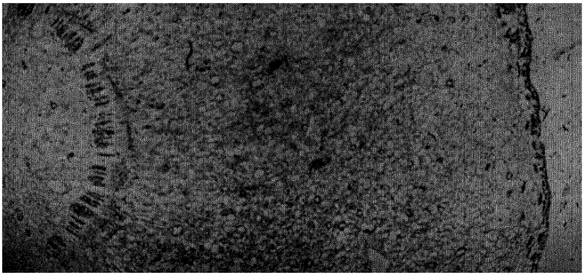


FIG. 316. Cross section of a portion of the stem of Zamia.

produced cork cells on its outer side, the cortex and epidermis are sloughed off.

308. Spore-formation. The spore-bearing leaves (*sporophylls*) of Zamia differ greatly in appearance and structure from foliage leaves. They are borne compactly arranged on the terminal portions of short branches growing from the apical region of the stem. Zamia has two kinds of spores distinguished, on the basis of their size, as *macrospores* and *microspores.* The sporangium that contains the larger spores (macrospores) is a *macrosporangium,* the leaf on which this sporangium is borne is a *macrosporophyll,* and the terminal portion of the branch on which macrosporophylls are borne is a *carpellate strobilus.* In like manner, the sporangium that contains the smaller spores (microspores) is a *microsporangium,* the leaf on which this sporangium is borne is a *microsporophyll,* and microsporophylls are borne on a *staminate*

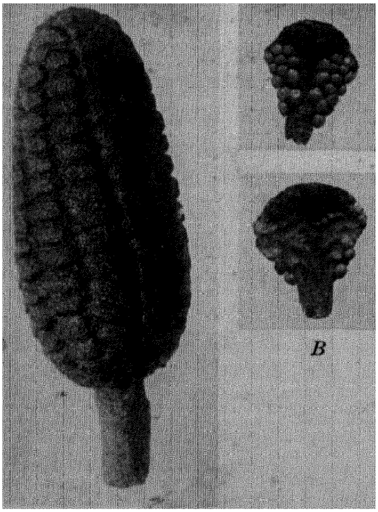


FIG. 317. *A*, staminate strobilus of Zamia. *B*, microsporophylls bearing on their lower surfaces many microsporangia.

strobilus. Any one plant produces only carpellate or only staminate strobili.

A staminate strobilus (Fig. 317) bears on its central axis many horizontally placed, closely packed microsporophylls. Each microsporophyll is almost scale-like and bears on its lower surface from 30 to 40 small microsporangia. Within each microsporangium (Fig. 318), as within the sporangia of ferns, spore mother cells are produced, and the division of each microspore mother cell gives

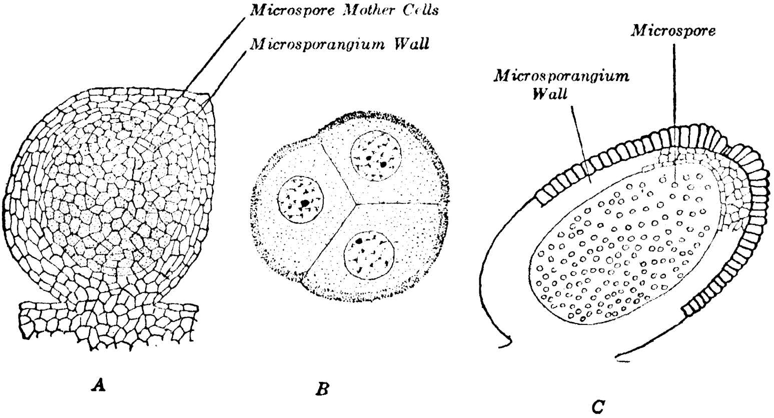


FIG. 318. *A*, vertical section of a young microsporangium of Zamia containing microspore mother cells. *B*, spores resulting from the division of a microspore mother cell. *C*, mature microsporangium.

rise to four microspores. Since each microsporangium produces approximately 500 microspores, and since there are, on an average, perhaps 35 microsporangia on each of the 200 or more microsporophylls, the number of microspores produced on a single plant is enormous.

A carpellate strobilus (Fig. 319) is larger than a staminate strobilus, and consists of a central axis bearing macrosporophylls. A macrosporophyll is larger and fleshier than a microsporophyll. When mature, it consists of a stalk and an expanded outer portion; to the inner side of the latter—that is, to the side toward the central axis of the strobilus—are attached two *ovules.*

An ovule (Fig. 320, *A*) begins its development as a bluntly conical protuberance, the *nucellus* (or macrosporangium), on the inner surface of the expanded portion of the young macrosporophyll. From its base an enclosing *integument* grows upward and

about the nucellus but leaves a small tubular opening, the *micropyle*, leading to the outer end of the nucellus. The integument seems to be a distinct organ, the sporangium proper being only the nucellus. But since nucellus and integument are closely combined, the two together are commonly treated as a single structure, the

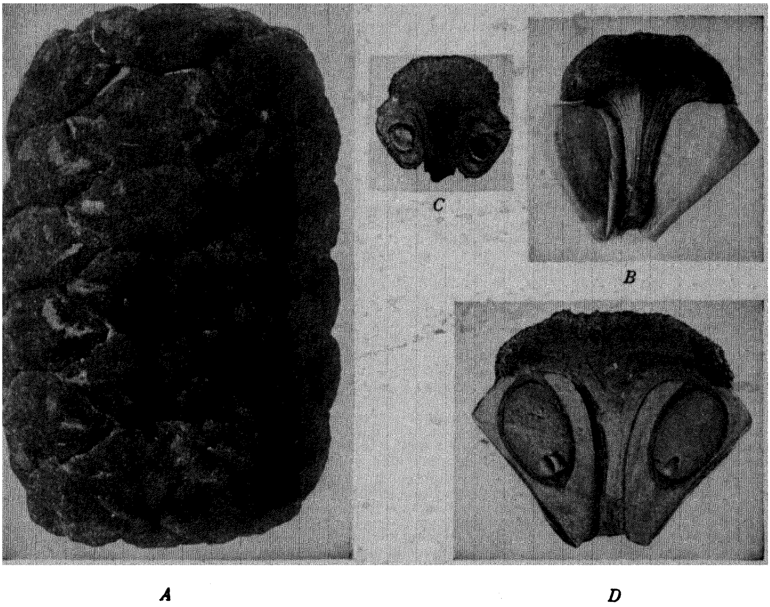


FIG. 319. *A*, carpellate strobilus of Zamia. *B*, macrosporophyll bearing 2 ovules. *C*, lengthwise section of a young macrosporophyll, showing an early stage in the development of macrogametophytes. *D*, similar section at a later stage; macrogametophytes fully developed.

ovule. As development continues, a small depression (*pollen chamber*) is developed at the end of the nucellus next the micropyle.

Only one macrospore mother cell becomes differentiated within the nucellus, and so but four macrospores are formed. These macrospores lie in an axial row in the central part of the nucellus.

309. Macrogametophyte (Fig. 320, *B*, *C*). Two fundamentally important features of seed plants are that the macrospore is firmly and permanently enclosed within the macrosporangium, and that the macrogametophyte develops to maturity entirely within the macrospore wall. Although four macrospores are formed within the macrosporangium, but one, usually that farthest from the

micropyle, develops into a macrogametophyte; the other three soon disintegrate.

The development of the macrogametophyte begins with a series of nuclear divisions. Later, by cell division it becomes many-celled, and by further cell division and growth the gametophyte increases in size. Meanwhile the nucellus and integument are

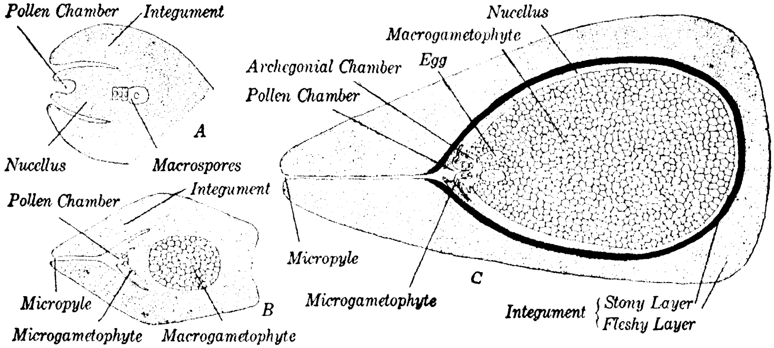


FIG. 320. Zamia; stages in the development of a macrogametophyte. *A*, 4 macrospores are formed. *B*, 1 macrospore has geminated to form a macrogametophyte. *C*, just before gametic union.

growing; but the macrogametophyte is developing at the expense of the adjoining cells of the nucellus, some of the nucellar tissue being digested and broken down. As the macrogametophyte develops further, a small depression, the *archegonial chamber*, appears in the end toward the micropyle. Two to six archegonia are formed at this end of the macrogametophyte, each opening into the archegonial chamber. An archegonium consists of two neck cells and a very large egg, the latter imbedded in the tissue of the macrogametophyte.

310. Microgametophyte (Fig. 321). The development of a microgametophyte from a microspore begins while the latter is still within the microsporangium. The microspore divides to form two daughter cells of unequal size. The smaller is the *prothallial cell,* so called because this single cell is thought to correspond to the vegetative tissue of a fern prothallium; the other and larger cell soon divides into a small *generative cell* and a large *tube cell.* Both these divisions occur within the microspore wall. The development of the microgametophyte now ceases for a time. This three-celled immature microgametophyte is a *pollen grain.*

The microsporangium now breaks open, and the pollen grains are distributed by winds. Some of the dust-like grains may be blown to a carpellate strobilus. At this time, in consequence of an elongation of the central axis of the carpellate strobilus, the macrosporophylls are not closely pressed together. Some pollen grains, therefore, may sift between the macrosporophylls and

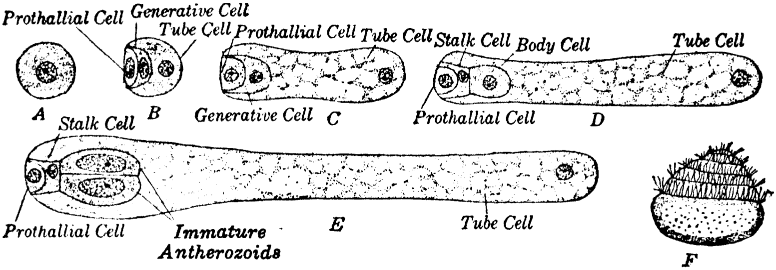


FIG. 321. Zamia; stages in the development of a microgametophyte. *A*, *B*, stages passed through in the microsporangium; *C–F*, while the pollen tube is growing through the nucellus. *A*, microspore. *B*, 3-celled microgametophyte (pollen grain) at the time of its liberation from the microsporangium. *C*, early stage in the "germination" of a pollen grain. *D*, the generative cell has divided into stalk and body cells. *E*, the body cell has divided to form 2 antherozoids. *F*, mature antherozoid.

lodge in the vicinity of the ovules. At the outer end of the micropyle of each ovule is a drop of a sticky liquid in which some pollen grains become caught. Later this liquid, with the imprisoned pollen grains, is withdrawn through the micropyle to the pollen chamber (Fig. 320, *B*).

The transportation of young microgametophytes from the microsporangium to a specific place in the vicinity of the macrogametophyte (a process known as *pollination*) is one of the features especially characteristic of seed plants. The dependence of Zamia upon wind pollination necessitates the production of a very large number of pollen grains, since the vast majority of grains will not be carried to a place where they can function.

After the pollen grains reach the pollen chamber, their development is resumed. This further development (the "germination" of a pollen grain) begins with an elongation of the tube cell into a cylindrical *pollen tube* which grows into the nucellus and absorbs food materials for the further growth of the microgametophyte. Several pollen grains may germinate in the pollen chamber

and develop tubes. The generative cell divides into a *stalk cell* and a *body cell.* The body cell in turn divides to form two cells that ultimately become antherozoids. An antherozoid has approximately the shape of a top; beginning at its pointed end is a spiral groove of several turns, and from the base of this groove grow a great number of flagella.

311. Gametic Union. At the time of pollination the macrogametophyte is still in an early stage of development. The completion

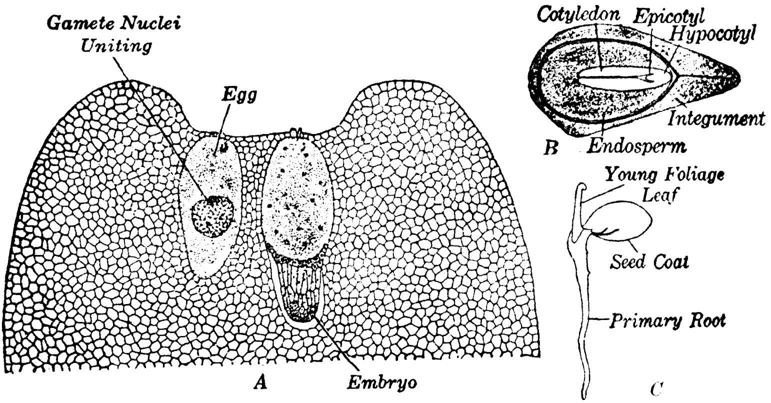


FIG. 322. Zamia. *A*, apical portion of a macrogametophyte; gamete nuclei uniting at the left; at the right a young embryo. *B*, lengthwise section of a seed. *C*, young sporophyte developing from a germinating seed.

of its development requires several months, during which time the pollen tube is growing in the nucellus. Finally, when the macrogametophyte and eggs are mature, the basal end of the tube—that is, the end still in the pollen chamber—grows through the nucellus directly to the archegonial chamber, and the end of the tube bursts. Since several tubes usually reach the archegonial chamber, a number of antherozoids may be discharged into, and swim about in, the liquid of the chamber. These antherozoids, or some of them, make their way through the necks of the archegonia and unite with the eggs (Fig. 322, *A*)—only one antherozoid uniting with any one egg.

312. Development of a Seed. The nucleus of the zygote now divides, and the daughter nuclei by repeated divisions give rise to a many-nucleate *proembryo.* Still later, cell divisions occur, chiefly between those nuclei of the proembryo which lie in its

basal part. Some of the uppermost of the cells so formed elongate and push the basal portion of the proembryo deep into the tissue of the macrogametophyte. The elongating cells form a long, slender, much-coiled *suspensor*. The cellular mass which is thrust, by the growth of the suspensor, deep into the macrogametophyte and which feeds upon the cells of the macrogametophyte is the embryo. The proembryo has, in this manner, become differentiated into embryo and suspensor. The embryo continues to grow and develop slowly.

The whole structure ultimately developed from the ovule and its inclusions is a *seed* (Fig. 322, *B*). It consists of:

(*a*) The embryo—the new sporophyte—which becomes differentiated into two large primary leaves (*cotyledons*) and a central axis. The part of this axis below the level of attachment of the cotyledons is the *hypocotyl;* the part above, a small mass of embryonic tissue, is the *epicotyl.* The suspensor is still discernible, attached to the end of the hypocotyl.

(*b*) A large mass of nutritive tissue or *endosperm* filled with reserve foods. The endosperm is the persisting tissue of the macrogametophyte.

(*c*) A *seed coat,* composed of an outer fleshy layer and an inner stony layer, both developed from the integument. A thin, papery layer immediately about the endosperm is derived chiefly from the nucellus. The integument and the nucellus are parts of the old sporophyte. The seed, therefore, consists of structures belonging to three distinct generations—the new sporophyte, the macrogametophyte, and the old sporophyte.

313. Germination of a Seed (Fig. 322, *C*). By the time the seeds are mature, a shriveling of the macrosporophylls makes it possible for the seeds to drop from the strobilus and to fall to the ground. Under suitable conditions they may later germinate. In germination, a seed absorbs water and the embryo contained in it continues growth. The hypocotyl elongates and pushes out through the micropylar end of the seed coat, bending, if necessary, in order to grow downward into the soil. The terminal portion of the hypocotyl forms the primary root. Although the cotyledons remain partly within the seed coat, they elongate sufficiently to free their basal portions and the epicotyl. The stem and leaves eventually develop from the epicotyl, except that the lowermost portion of the stem is derived from the hypocotyl.

Until this time the young sporophyte has been unable to manufacture its own carbohydrates, and has been dependent upon reserve foods stored in the endosperm (macrogametophyte)—foods that were derived by the macrogametophyte from the cells of the parental sporophyte. As soon as the epicotyl has de-

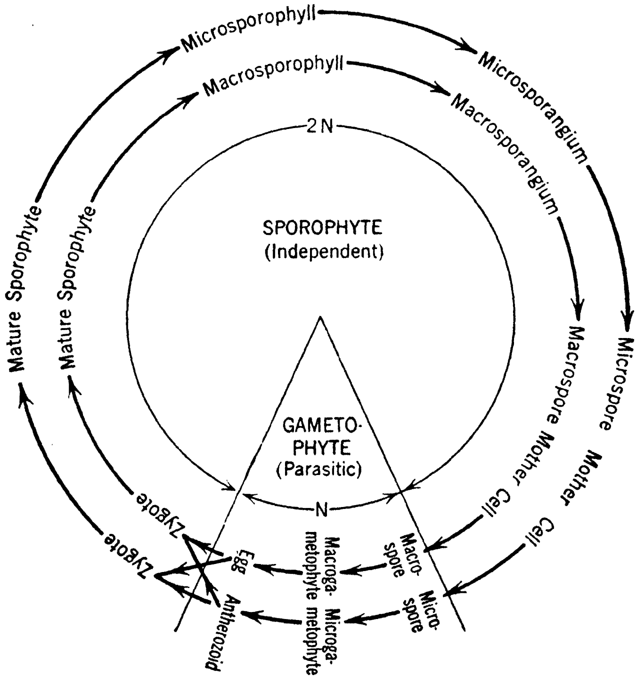


FIG. 323. Life cycle of Zamia.

veloped chlorophyll-containing leaves, the young sporophyte is independent.

314. Life Cycle (Fig. 323). Two sporophytic plants are necessary in the life cycle of Zamia. One sporophyte bears staminate strobili, microsporophylls, microsporangia, and microspores. Another sporophyte bears carpellate strobili, macrosporophylls, ovules (macrosporangia with integuments), and macrospores. A microspore develops into a microgametophyte which produces antherozoids; a macrospore into a macrogametophyte which produces archegonia and eggs. The union of an antherozoid with an egg forms a zygote. After gametic union a proembryo is formed

whose apical portion develops into an embryo. The embryo and the surrounding structures of the ovule mature into a seed. On germination the embryo within the seed develops into either a staminate or a carpellate sporophyte.

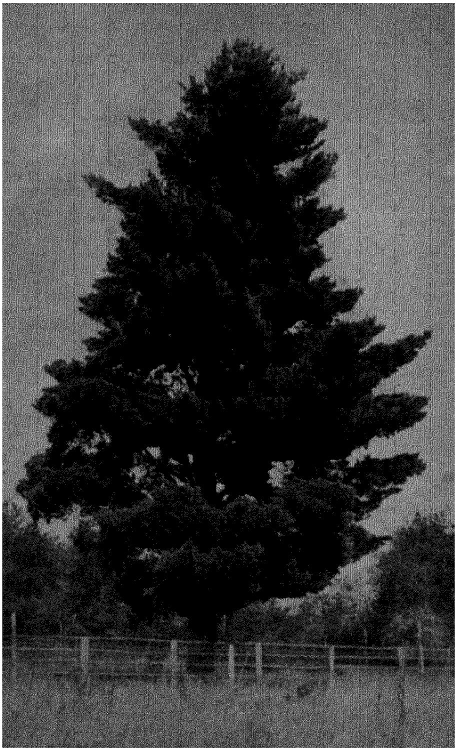


FIG. 324. Pine; a mature sporophyte. Photograph by L. S. Cheney.

THE PINE

315. Stem. The Coniferales, which include the pines, are the largest order of gymnosperms both in number of species and in number of individuals. In the temperate regions of the northern hemisphere, Coniferales form forests of vast extent. Most of the lumber sold in the United States is sawn from trunks of coniferous trees. In fact, the demand for this type of lumber has so far outstripped the supply that there are but small remnants of available coniferous timber left in the north central and north Atlantic states. There are still extensive coniferous forests in the Pacific states and in the South.

The pine tree (Fig. 324) is the sporophytic generation. Since its terminal bud grows more rapidly than the terminal buds of the branches, a conspicuous central trunk is formed. The lateral buds which are to develop into *long branches* are borne in whorls. The gradual transition in length of these branches from the lowermost and longest to the uppermost and shortest gives the tree as a whole, when it stands in the open, a conical form. If it grows in a dense

stand, however, the tree bears branches in its upper portion only, the lower branches having died and fallen early.

In addition to long branches, the pine has branches of another sort (*spur branches*, Fig. 325) which, although they may live for a number of years, remain very short and slender. It is at the ends of these spur branches that the needle-shaped foliage leaves are borne.

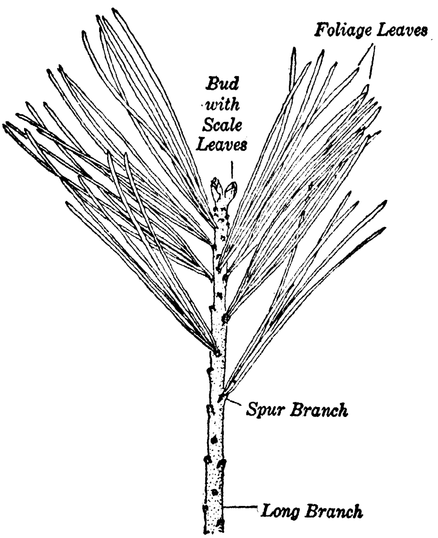


FIG. 325. Apical portion of a stem or branch of the white pine.

The primary tissues of a young pine stem (Figs. 326, 327) consist of stele, cortex, and epidermis. At the center of the stele is a pith, surrounded by a cylinder of vascular bundles separated from one another by medullary rays. The conducting elements of the primary xylem are tracheids. The pine, like most other gymnosperms, produces no vessels. The phloem consists of thin-walled sieve tubes intermingled with a few shorter but broader thin-walled cells. Between the xylem and the phloem of each bundle is a cambium. The cortex is composed of rounded thin-walled cells which, at least in the outer portion of the cortex, frequently contain chloroplasts. Here and there in the cortex and xylem are longitudinal resin canals. The outermost layer of the stem is a heavily cutinized epidermis.

Growth in thickness of the stem is due mainly to the formation of secondary xylem and secondary phloem by cambial activity. The tracheids produced by the cambium are of much the same size as those in the primary xylem. Since the tracheids produced at the beginning of each growing season are somewhat larger than those developed later in the year, there are well-defined annual rings in the secondary xylem (Fig. 40). It is chiefly because of the approximate uniformity in size of the tracheids and because of the hardness of their walls that the pine is so valuable as a source of

lumber. The original medullary rays are continuous through the secondary xylem. The cambium gives rise to new medullary rays from time to time, so that the later-formed rings of xylem contain many more rays than do those parts of the xylem formed earlier.

The portion of a medullary ray within the xylem contains relatively short living thin-walled cells which at certain seasons are filled with reserve foods; in some species it contains also thick-

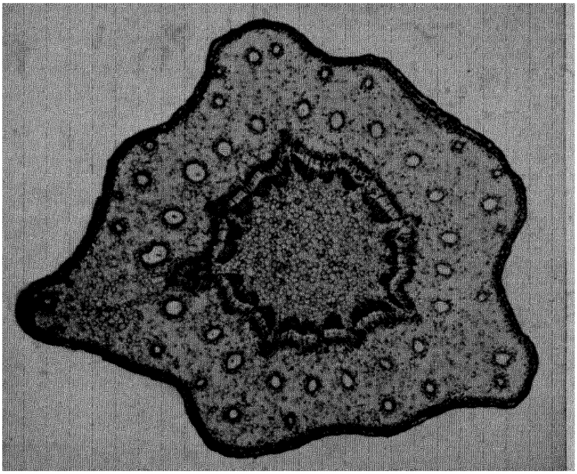


FIG. 326. Cross section of a young pine stem. The primary bundles are evident, although cambial activity has begun.

walled tracheids whose function is the lateral transport of liquids. In the portion of a ray within the phloem, all the cells are living and thin-walled. Resin canals are formed here and there in the secondary xylem, extending for considerable distances up and down the stem. These canals appear in cross section as large pores bordered by thin-walled cells, and are connected by other resin canals that run approximately horizontally in the medullary rays. The secondary phloem cells ordinarily remain functional for only a year, the phloem of previous years persisting as a crushed mass of cells outside that formed later.

At about the time that cambial activity begins in the stele, a cork cambium is developed in the cortex just beneath the epidermis. This cork cambium functions for a time; later, additional

cork cambiums are developed, as in dicotyledonous stems. By the activity of the various cork cambiums and by the formation of new phloem, a thick bark is formed that surrounds the xylem.

316. Roots. In a young portion of the mature region, the stele of a pine root includes two xylem and two phloem strands. These xylem and phloem strands alternate, forming an interrupted cylinder. Later, a central strip of thin-walled cells between the two

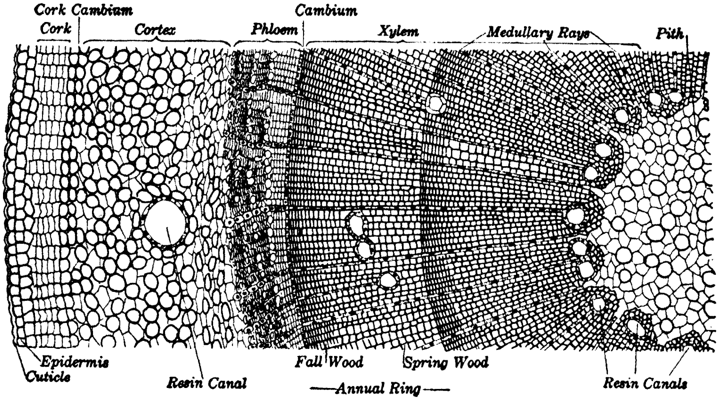


FIG. 327. Cross section of a portion of an older pine stem, showing its component tissues.

xylem strands also becomes xylem. The young stele now includes a thin plate of primary xylem a few cells in thickness flanked on either side by a plate of primary phloem, the region between primary xylem and primary phloem being occupied by thin-walled cells. The outer portion of the stele is a pericycle, several cells in thickness. The cortex and epidermis resemble those of a dicotyledonous root.

As the root grows older, certain strips of thin-walled cells between primary xylem and primary phloem begin to function as a cambium; still later, cambial activity extends to the cells of the pericycle just outside each edge of the xylem plate. The primary xylem is now completely surrounded by a cylinder of cambium. This cambial cylinder develops secondary xylem on its inner and secondary phloem on its outer side (Fig. 328), as does the cambium of the stem; an old root, therefore, has much the same appearance in cross section as an old stem. A cork cambium is formed from the outermost cells of the pericycle; after this cork cambium has

foliage leaves. They are borne compactly arranged on the terminal portions of short branches. The pine has two kinds of spores distinguished, on the basis of their size, as *macrospores* and *microspores.* The sporangium which contains the larger spores (macrospores) is a *macrosporangium,* the leaf on which this sporangium is borne is a *macrosporophyll,* and the terminal portion of the branch on which macrosporophylls are borne is a *carpellate strobilus.* In like manner, the sporangium which contains the smaller spores (microspores) is a *microsporangium,* the leaf on which this sporangium is borne is a *microsporophyll,* and microsporophylls are borne on a *staminate strobilus.* Any one sporophyte may produce both carpellate and staminate strobili.

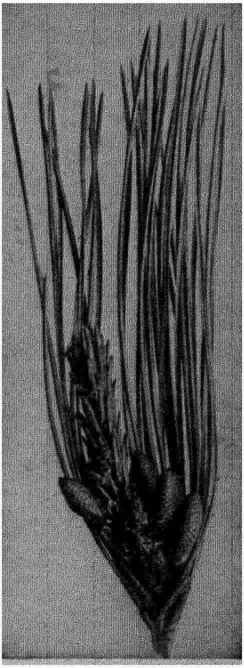


FIG. 330. Branch of a pine bearing staminate strobili.

Staminate strobili (Fig. 330) are produced in clusters near the ends of long branches. Each strobilus is comparatively small, rarely more than a half inch in length. It consists of a central axis bearing many horizontally disposed scale-like microsporophylls (Fig. 331). On the under side of each sporophyll, and with their long axes parallel to the long axis of the sporophyll, are two ovoid microsporangia. Within each microsporangium are produced many microspore mother cells, each of which by division gives rise to four microspores.

Cårpellate strobili (Fig. 332) are much larger than staminate strobili. A young carpellate strobilus has a central axis bearing numerous bracts. As the strobilus grows older (Fig. 333), a scale-like structure, several times the size of a bract, develops in the axil between each bract and the central axis. This scale bears two *ovules* on its upper surface. Opinions differ as to whether the scale is a macrosporophyll or whether it represents a reduced branch.

An ovule (Fig. 333, *C*) begins its development as a mass of embryonic tissue—the *nucellus* or macrosporangium—on the surface of a scale. From the base of the nucellus an enclosing *integument*

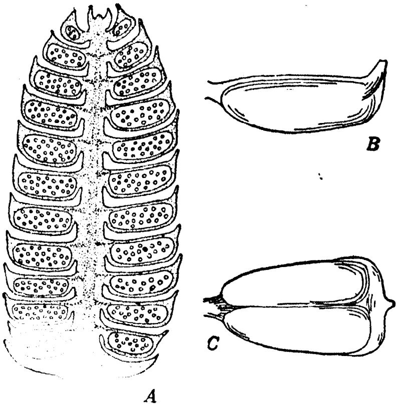


FIG. 331. Pine. *A*, lengthwise section of a staminate strobilus. *B*, *C*, microsporophylls viewed from the side and from below.

grows up and about it, leaving an opening, the *micropyle*. The integument seems to be a distinct organ, the sporangium proper being only the nucellus. The two together constitute an ovule. A very small depression (*pollen chamber*) is formed at the end of the nucellus next the micropyle.

A single macrospore mother cell becomes differentiated near the center of the nucellus. From this cell, by division, is later formed an axial row of four macrospores.

319. Macrogametophyte. Only one macrospore in a nucellus, usually that macrospore farthest from the micropyle, develops into a macrogametophyte; the other three macrospores soon disintegrate. The development of the functional macrospore into a macrogametophyte begins with a series of nuclear divisions (Fig. 334, *A*). Later, by cell division, a many-celled macrogametophyte is formed which, by the repeated growth and division of its cells, increases in size (Fig. 334, *B*, *C*). As a rule, two or three archegonia are formed at the micropylar end of the macrogametophyte. Each archegonium consists of four or eight neck cells and a very large egg, the latter being imbedded in the macrogametophyte.

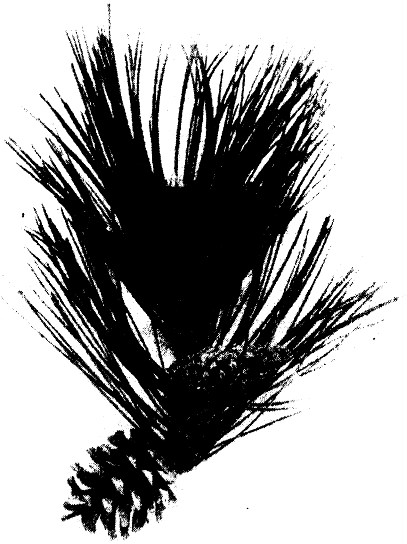


FIG. 332. Branch of a pine bearing carpellate strobili.

320. Microgametophyte and Gametic Union. The development of a microgametophyte from a microspore (Fig. 335, *A*, *B*) begins while the latter is still within the microsporangium. The microspore divides into a small *prothallial cell* and a much larger *apical cell;* a similar division of the apical cell forms a second small prothallial cell and a large cell, the latter still called an apical cell. Both prothallial cells begin to disintegrate soon after they are formed. The apical cell in time divides into a small *generative cell* and a large *tube cell.* It is at this four-celled stage (that of the tube cell, generative cell, and two disintegrating prothallial cells) that the partially developed microgametophyte (now a *pollen grain*) is shed. The pollen grain of the pine has two lateral inflated appendages ("wings") that give it buoyancy. These wings were developed from the wall of the microspore before it germinated to form a microgametophyte.

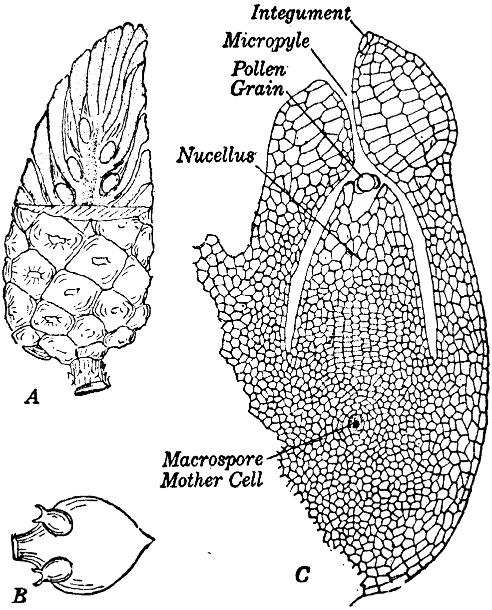


FIG. 333. Pine. *A*, carpellate strobilus. *B*, scale bearing 2 ovules. *C*, lengthwise section of an ovule; the macrospore mother cell is differentiated. *A* after Bessey.

The transfer of pollen from the opened microsporangia to the carpellate strobili (*pollination*) is brought about by winds. At about the time that pollen is being shed, the central axis of the carpellate strobilus elongates, separating the macrosporophylls which until this time had been closely pressed together. In consequence, some pollen grains may sift between the macrosporophylls and lodge in the micropyle. A growth in thickness of the apical portion of the integument now closes the micropyle and imprisons these pollen grains in the pollen chamber.

After the young microgametophyte reaches the pollen chamber,

its development is resumed. In this "germination" of the pollen grain (Fig. 335, *C*, *D*), the tube cell elongates into a *pollen tube* which penetrates the nucellus. The generative cell divides into a *stalk cell* and a *body cell.* By this time the prothallial cells have

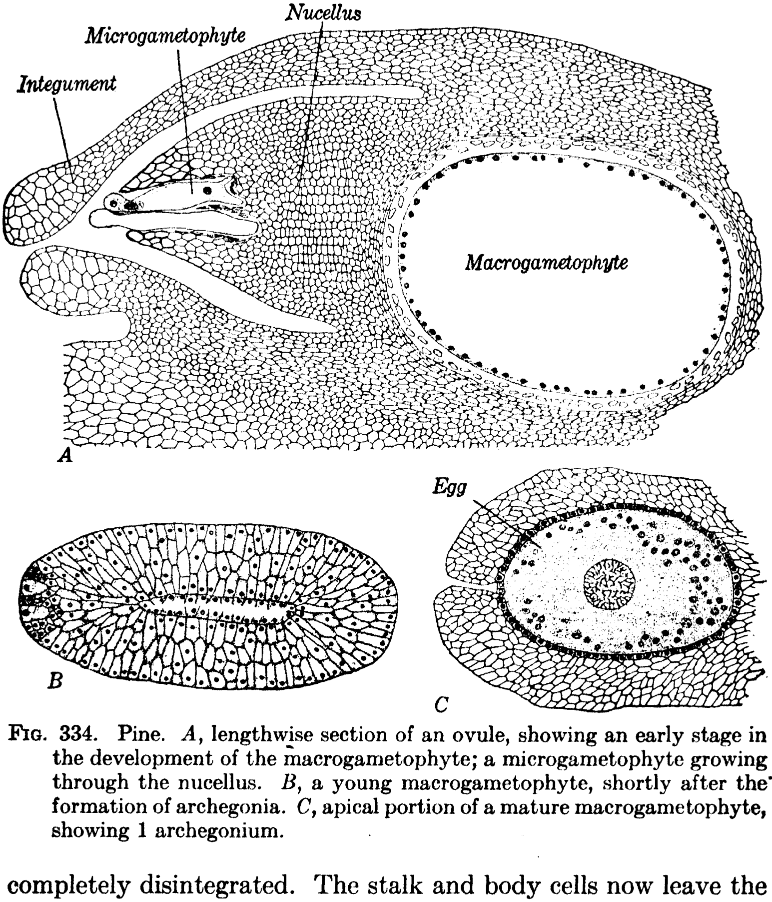


FIG. 334. Pine. *A*, lengthwise section of an ovule, showing an early stage in the development of the macrogametophyte; a microgametophyte growing through the nucellus. *B*, a young macrogametophyte, shortly after the formation of archegonia. *C*, apical portion of a mature macrogametophyte, showing 1 archegonium.

completely disintegrated. The stalk and body cells now leave the old wall of the pollen grain and migrate slowly down through the pollen tube. During this migration the body cell enlarges, and its nucleus divides to form two male gamete nuclei; it is not yet certain whether this nuclear division is followed by a division of the body cell. The end of the pollen tube grows through the nucellus to the macrogametophyte, and then to and through the neck of an archegonium. Finally the end of the tube bursts, and the

contents of the end of the tube (including the tube nucleus, the stalk cell, and the cytoplasm of the body cell containing the two male gamete nuclei) are discharged into the apex of the egg. One male gamete nucleus migrates to the egg nucleus (Fig. 336, *A*);

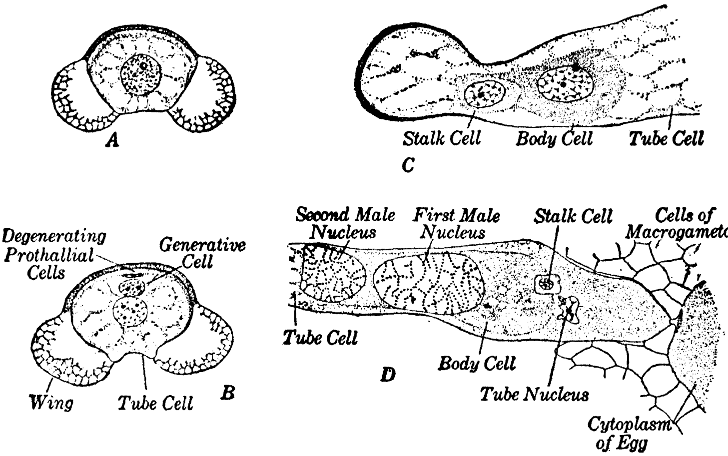


FIG. 335. Pine. *A*, microspore. *B*, microgametophyte (pollen grain) at the time of its liberation from the microsporangium. *C*, the generative cell has divided to form stalk and body cells. *D*, distal end of the pollen tube, shortly before gametic union. *C* and *D* after Miss Ferguson.

the remaining structures from the pollen tube, including the other male gamete nucleus, remain in the cytoplasm near the apex of the egg and eventually disappear.

321. Seed-development. After gametic union the zygote nucleus divides and the daughter nuclei divide. The four nuclei now present migrate to the base of the cytoplasm of the old zygote (now a *proembryo*), and come to lie in a plane at right angles to its long axis (Fig. 336, *C*, *D*). The four nuclei divide, their division being followed by a cell division that forms four basal one-nucleate cells; the four nuclei above this tier of cells are in what may be called *compartments*, each of which is delimited by walls at its lateral and basal sides, but is continuous above with the cytoplasm of the proembryo (Fig. 336, *E*). By another division of the four cells and four compartments the proembryo comes to consist of four tiers, three tiers of four cells each and one tier of four compartments (Fig. 336, *F*).

The proembryo now undergoes differentiation. The four cells

farthest from the neck of the archegonium (*apical cells*) develop into the embryo (or embryos); those of the next tier elongate greatly to form a *suspensor* that pushes the apical tier of cells deep into the macrogametophyte; the tier of four cells next above (*rosette cells*) forms a brace for the suspensor in the pushing of the

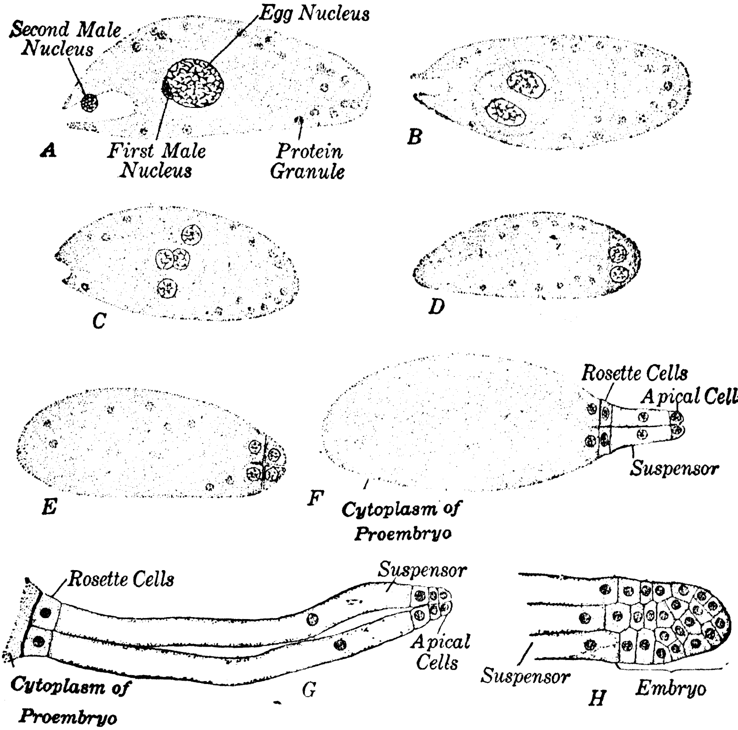


FIG. 336. Pine; gametic union and embryo-development. *A*, union of gamete nuclei. *B*, 2 nuclei, resulting from the division of the zygote nucleus, are now present. *C*, *D*, 4-nucleate proembryos (only 2 nuclei showing in *D*). *E*, proembryo with 4 cells and 4 "compartments." *F*, after the next cell division. *G*, the suspensor cells have elongated and the apical cells have divided. *H*, a single embryo at a later stage; 1 of 4 initiated by the separation and division of the apical cells of preceding stages.

apical cells into the macrogametophyte (Fig. 336, *G*, *H*). The compartments forming the uppermost tier eventually disintegrate, together with the remaining unused cytoplasm of the proembryo. Very commonly the whole structure splits vertically at an early

stage into four parts, each consisting of a vertical row of three cells (one apical, one suspensor, and one rosette cell). Thus four embryos may be developed from each zygote, but ordinarily only one reaches maturity, the other three embryos ceasing after a time to develop. The young sporophyte therefore can be traced back to the four apical cells, or to one of the four apical cells, differentiated from a proembryo. From the apical cell or cells of any embryo

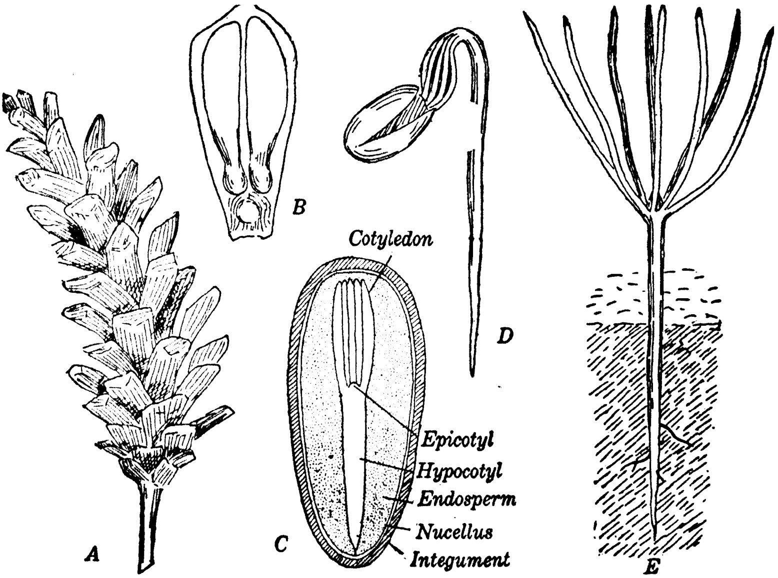


FIG. 337. *A*, carpellate strobilus (cone) of a pine at the time seeds are shed. *B*, scale with 2 seeds. *C*, lengthwise section of a seed. *D*, *E*, germination of a seed.

there is formed by division a many-celled mass which eventually becomes differentiated into *hypocotyl*, *epicotyl*, and *cotyledons*. The fully developed embryo (Fig. 337, *C*) is imbedded in the center of the macrogametophyte (now called the *endosperm*), and is nearly as long as the endosperm. The hypocotyl is conspicuous, and there are several cotyledons, the number varying with the species of pine; the epicotyl is still very small when the seed is mature.

The development of an embryo is accompanied by certain changes in the structures surrounding it. The endosperm (macrogametophyte) of the mature seed is larger and contains more re-

serve food than it did at the time of the union of gametes. The endosperm is surrounded by a thin layer, the remains of the nucellus. In the development of the seed the integument also is modified, its cells becoming stony and forming a hard *seed coat.* In many species of pine, a portion of the scale remains attached to each seed, forming a wing that assists in the dispersal of the seed by winds (Fig. 337, *B*).

After pollination, and until seeds are fully developed, the scales of the strobilus are closely appressed. When the seeds are mature, however, the scales again become separated from one another in consequence of the growth of the central axis of the strobilus (Fig. 337, *A*), the seeds then being free to fall from the strobilus.

322. Germination of a Seed (Fig. 337, *D, E*). A pine seed may germinate in the spring following its maturation; or it may remain dormant for several years if conditions are not favorable for germination. When conditions are suitable, the seed absorbs moisture and the embryo resumes growth. The end of the hypocotyl pushes its way through the seed coat, bending if necessary in order to grow downward into the soil. The cotyledons now emerge from the seed coat, and the portion of the hypocotyl adjacent to the cotyledons bends and grows upward. When they emerge from the seed coat the cotyledons spread apart and become green. Growth to this stage has been accomplished by the absorption of water and the use of foods stored in the endosperm; after the cotyledons develop chlorophyll, the young sporophyte, being able to manufacture foods, becomes independent of the endosperm. The foods manufactured by the cotyledons are used in the development of the epicotyl and the adjoining part of the hypocotyl into a stem and in the development of the terminal portion of the hypocotyl into a root. After the portion of the stem derived from the epicotyl has developed secondary leaves, the cotyledons eventually disappear, the secondary leaves now performing the photosynthetic work of the plant. The young plant may now, by the growth and development of its parts, and by the formation of new branches, leaves, and roots, become a mature sporophyte or pine tree.

323. Life Cycle (Fig. 338). The sporophyte (pine tree) produces staminate and carpellate strobili. A staminate strobilus bears many microsporophylls on each of which are two microsporangia. In a microsporangium are formed many microspore mother cells. Each microspore mother cell divides to form four microspores.

A microspore develops within the sporangium into a young male gametophyte (pollen grain).

A carpellate strobilus bears many macrosporophylls each producing two ovules. An ovule is a macrosporangium covered by an integument. Within a macrosporangium (nucellus) one macrospore mother cell is differentiated; this divides to form four macrospores.

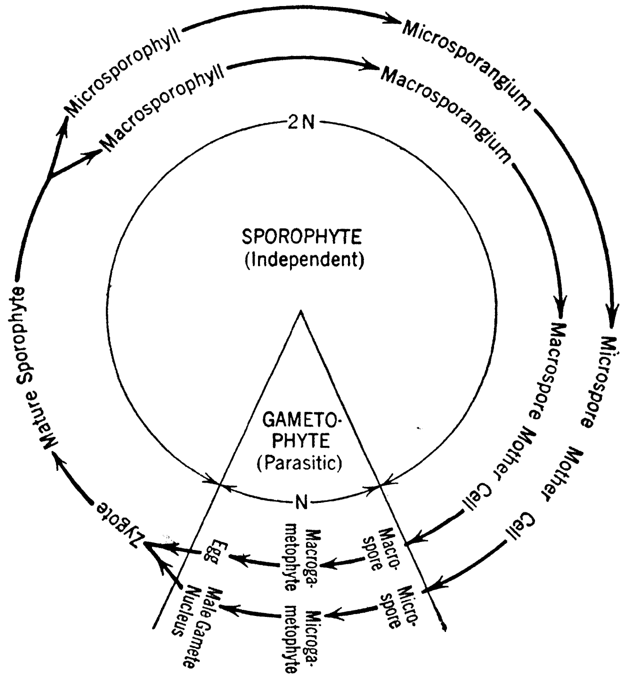


FIG. 338. Life cycle of a pine.

Of these, three degenerate. The persisting macrospore grows into a macrogametophyte which bears archegonia.

A pollen grain reaching the nucellus develops a pollen tube within which two male gamete nuclei are formed. The pollen tube finally penetrates an archegonium and liberates the male gamete nuclei. After gametic union a cellular proembryo develops from the zygote and becomes differentiated into embryo and suspensor. By further development the embryo forms epicotyl, hypocotyl, and several cotyledons. The ovule has become a seed, in which the embryo lies enclosed by the endosperm (macrogametophyte),

which in turn is covered by the remains of the nucellus and by a seed coat derived from the integument.

When the seed germinates, the embryo resumes growth, developing into a long-lived pine tree. This produces branches, leaves, roots, and eventually staminate and carpellate strobili.

324. New Features in Gymnosperms. Gymnosperms stand higher in the evolutionary scale than do pteridophytes. Important new features developed by such gymnosperms as Zamia and pine are:

(*a*) The production of two kinds of strobili which bear respectively microsporophylls and macrosporophylls.

(*b*) The retention for a time of the developing microgametophytes (pollen grains) in the microsporangium.

(*c*) The permanent retention of the macrospore and the macrogametophyte within the macrosporangium (nucellus).

(*d*) The development of a covering (integument) about each macrosporangium.

(*e*) A further simplification of the microgametophyte.

(*f*) Pollination and the formation of a pollen tube.

(*g*) Direct parasitism of both gametophytes upon the sporophyte.

(*h*) The establishment of the seed habit.

CHAPTER XXIX

ANGIOSPERMS

325. General Characteristics. Angiosperms are still more highly specialized than are gymnosperms. They present, therefore, the highest evolutionary development reached, to the present time, by any plants. Fossil remains of angiosperms are found only in the later geological formations, and it seems clear that as a group they are more modern than are bryophytes, pteridophytes, or gymnosperms. Angiosperms include most of the familiar cultivated plants, "wild flowers," and weeds; and, with the exception of conifers, almost all trees and shrubs.

Angiosperms are distinguished from gymnosperms by the fact that their seeds, instead of being exposed, are produced within an enclosing organ (the fruit). The general structure of the vegetative parts of the sporophytic generation of angiosperms has been discussed in Chapters IV–VII. There remain for consideration the gametophytes, and those portions of the sporophyte—namely, the flower, fruit, and seed—which are intimately associated with the gametophytes.

326. Structure of a Flower (Fig. 339). A flower, like a strobilus, is a branch (or the terminal portion of a branch or stem) which bears sporophylls. The flowers of all angiosperms are alike in that each possesses one or more sporophylls. There are great differences between the flowers of different angiosperms, however, in number, size, and arrangement of sporophylls, and in number, size, shape, and color of other lateral appendages (floral leaves) if these are present. In nearly all flowers the lateral structures (including sporophylls) are arranged in spirals or concentric circles (whorls) upon a shortened, somewhat flattened axis.

In a flower, such as one of the apple, primrose, strawberry, violet, or trillium, which has all the characteristic parts, the following structures are present:

(*a*) An outer set of green floral leaves (*sepals*) which enclose the other parts of the flower until these are nearly mature. The sepals together comprise the *calyx*.

(*b*) An inner set of showy colored or white leaves (*petals*), constituting the *corolla*. In many flowers the petals aid in attracting the attention of insects which assist in pollination.

(*c*) A set of *stamens* (microsporophylls) within the petals.

(*d*) At the center of the flower, one or more *carpels* (macro-

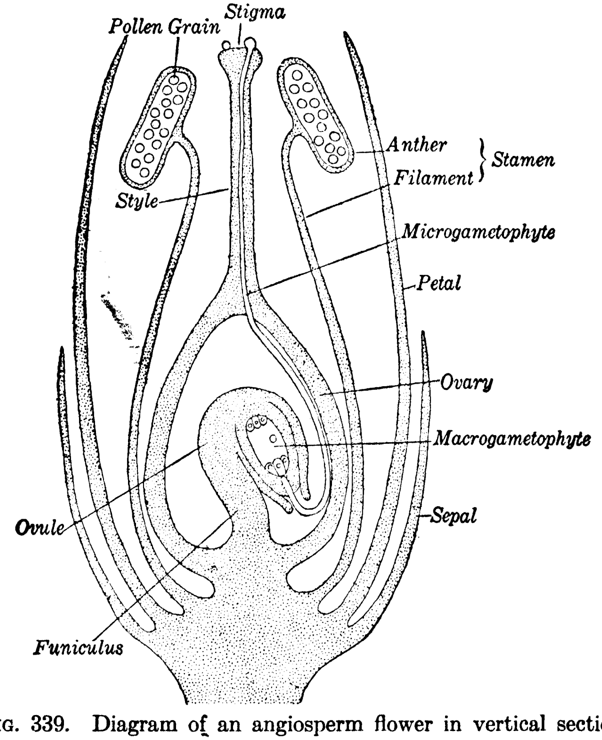


FIG. 339. Diagram of an angiosperm flower in vertical section.

sporophylls), constituting a *pistil* or pistils. Some flowers, such as that of the strawberry, have many pistils.

(*e*) A *receptacle*, the terminal portion of the branch or stem, which bears the calyx, corolla, stamens, and pistil or pistils.

327. Evolution of Flowers. While angiosperms, as a group, are the most highly specialized of all plants, yet within the group there are important differences in degree of specialization. Especially is this true with respect to the organization of the flowers of various angiosperms.

It is probable that the flowers of primitive angiosperms bore a general resemblance to gymnosperm strobili; each consisting

of an elongated central axis bearing many spirally arranged sporophylls and having nothing closely corresponding to sepals or petals. It is uncertain whether the primitive angiosperm flower bore both macrosporophylls and microsporophylls, or whether each flower bore sporophylls of but one kind. Beginning with such a strobilus-like structure, the following general tendencies seem to have marked the evolution of flowers in different families of angiosperms:

(*a*) The differentiation of accessory leaves—sepals, or sepals and petals—borne below the sporophylls.

(*b*) An advance from a spiral arrangement of each set of floral parts (sepals, petals, stamens, and carpels) to a cyclic arrangement of one or more sets.

(*c*) A reduction of the large and indefinite numbers of floral parts to smaller and definite numbers.

(*d*) A shortening of the receptacle, accompanying steps *b* and *c*. The receptacle became broadened and flattened, or in some lines of descent concave.

(*e*) An advance from a condition in which all the members of any particular set of floral parts are alike and symmetrically arranged around a central axis (a condition of *radial symmetry*) to one in which the members of at least one set differ among themselves in size and shape, so that there is only one plane in which the flower can be divided into two equal parts (a condition of *bilateral symmetry*).

(*f*) An advance from a condition in which all the members of each set of floral parts are distinct and separate to one in which they are united in varying degrees with one another or with members of another set or sets.

The advances in these different lines have often not been at the same rate in the ancestry of any particular family or order, and related species in any such group may show very different degrees of advancement in floral structure. It is true also that in any single line of descent advance has gone on at different rates with reference to different sets of floral members; so that the flowers of any particular species may be advanced in one respect and primitive in another.

328. Stamens. A stamen (microsporophyll) consists usually of a more or less elongated stalk-like *filament* and an enlarged lobed *anther* which is borne at the apex of the filament. Within the anther

are a variable number of *pollen sacs* (microsporangia). Very commonly the young anther is two-lobed and each lobe contains two pollen sacs. Within each young pollen sac of an angiosperm, as within a microsporangium of Selaginella or of a gymnosperm, are produced a number of microspore mother cells (Fig. 340). These are surrounded by a conspicuous layer of nutritive cells. Each

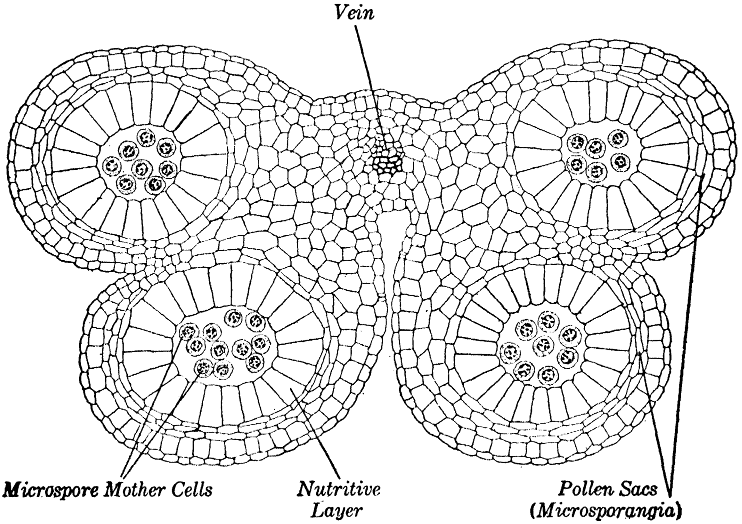


FIG. 340. Diagrammatic cross section of an anther before the division of microspore mother cells.

microspore mother cell, by two successive divisions (reduction divisions), gives rise to four microspores. While the microspore mother cells are dividing, the cells of the nutritive layer and some of the adjoining cells of the anther disintegrate. If there are two pollen sacs in each lobe, the tissue between them also often disintegrates. While the microspores are developing into pollen grains (§ 331), a longitudinal strip of special tissue is, in many angiosperms, differentiated on the outer face of each lobe of the anther. The lengthwise splitting of the anther along this strip (Fig. 341) permits the escape of the pollen grains from the pollen sacs. In some plants, as in the potato, the anther opens by a terminal slit or pore.

329. Pistils. A pistil is usually differentiated into three regions (Fig. 339): a swollen, hollow basal portion, the *ovary;* a narrow,

more or less elongated portion, the *style;* and, at the apex or along the side of the style, the *stigma*. In certain flowers the pistil has no

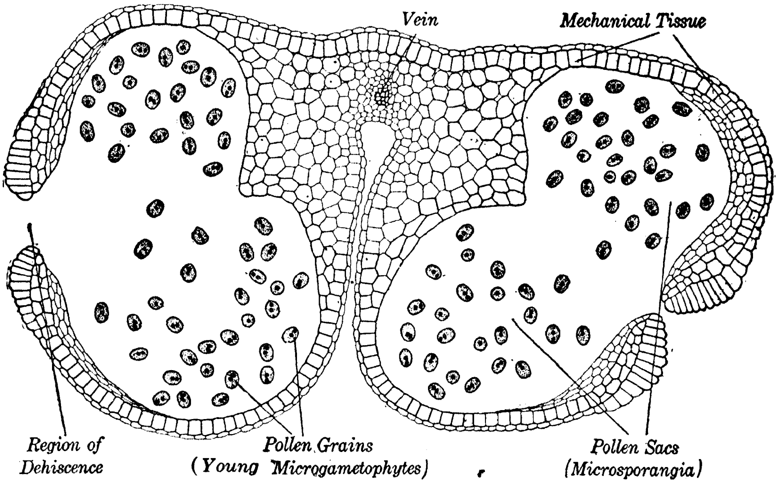


FIG. 341. Diagrammatic cross section of an anther at the time of the liberation of pollen grains.

style, and the stigma is attached directly to the upper portion of the ovary.

A pistil consisting of one carpel (macrosporophyll) only is a *simple pistil* (Fig. 342, *A*). In such a pistil the margins of the carpel

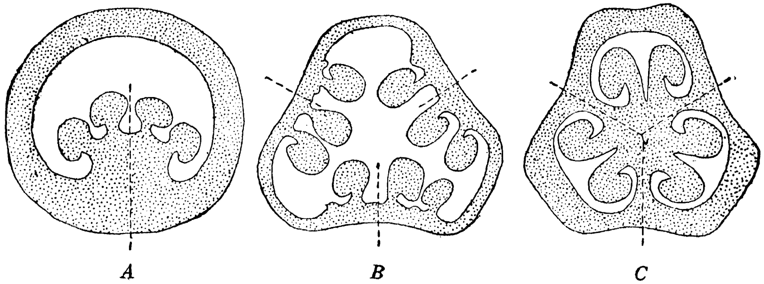


FIG. 342. Cross sections of ovaries, the united margins of the carpel or carpels being indicated by dotted lines. *A*, may apple; a simple ovary. *B*, violet; a compound ovary with a single cavity. *C*, lily; a compound ovary with as many cavities as carpels.

are usually so united—as in the bean or pea—as to enclose a single cavity. A pistil may, however, be formed by the union of two or

more carpels (Fig. 342, *B*, *C*). The ovary of such a *compound pistil* may enclose one or more than one cavity. For instance, the pistil of a lily or of a hyacinth is made up of three carpels united in such a way as to form three cavities within the ovary. In the pistil of

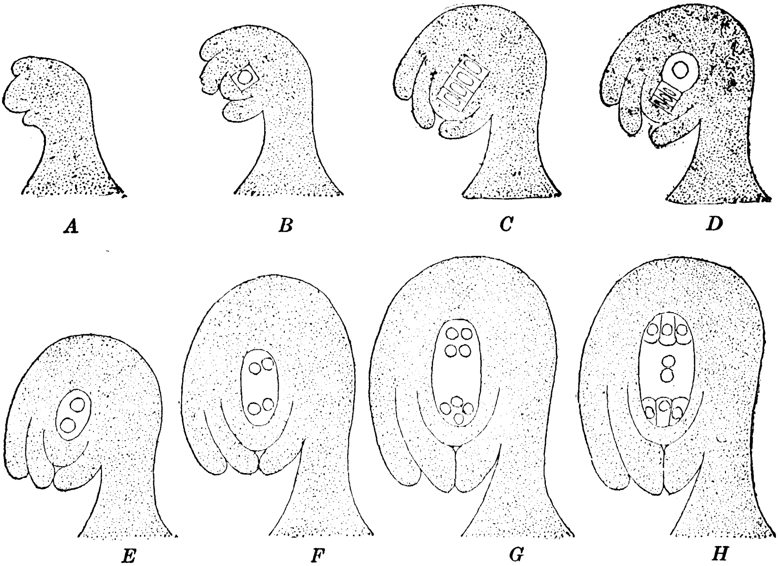


FIG. 343. Diagrams showing, in lengthwise section, the development of an ovule (including macrosporangium) and macrogametophyte. *A*, very young ovule; the inner integument has appeared. *B*, both integuments are present; the macrospore mother cell is differentiated. *C*, the nucellus is nearly enclosed by the integuments; the macrospore mother cell has divided to form 4 macrospores. *D–H*, successively later; the stages of macrogametophyte-development in *D*, *E*, *F*, *G*, and *H* respectively correspond to those shown in *A*, *B*, *C*, *D*, and *E*, Figure 344.

the violet, three carpels are so united that there is but a single cavity.

Within the cavity or cavities of the ovary are one or more *ovules*. Since the ovules are enclosed, pollen grains can not come into direct contact with them. This condition is very different from that in gymnosperms, whose pollen grains eventually reach the ovules. The difference in this respect is a fundamental one between gymnosperms and angiosperms.

An ovule (Fig. 343) may arise from the base of the ovary or from the inner surface of a carpel. As in gymnosperms, the nucellus (macrosporangium) is the first part of the ovule to develop. From

the basal portion of the nucellus one or two integuments grow up and around it, leaving a passage-way (the micropyle) at the apex. Each ovule has a distinct stalk, the *funiculus*.

330. Macrospores and Macrogametophyte. The most frequent course of events within an angiosperm ovule is the following. A single macrospore mother cell is differentiated within the nucellar tissue (Fig. 343, *B*). This cell by two successive divisions

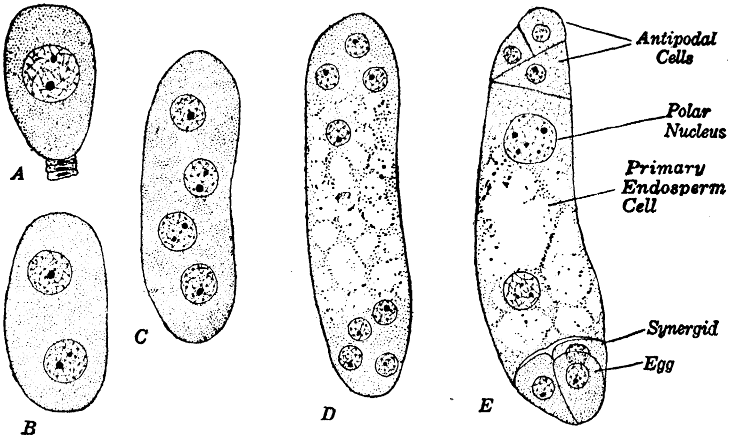


FIG. 344. *A*, beginning of the development of a macrospore (still 1-nucleate) into a macrogametophyte. *B–D*, 2-, 4-, and 8-nucleate stages in the development of a macrogametophyte. *E*, mature macrogametophyte. All figures diagrammatic.

(reduction divisions) gives rise to four macrospores which lie in an axial row within the nucellus (Fig. 343, *C*). One macrospore, usually that farthest from the micropyle, develops into a macrogametophyte; the other three macrospores disintegrate. The functional macrospore enlarges greatly (Fig. 344) and its nucleus divides; the two daughter nuclei eventually lie near the opposite ends of the cell; each of these daughter nuclei divides, and their daughter nuclei in turn divide. The macrogametophyte is now a large eight-nucleate cell, four of its nuclei lying in the micropylar end of the cell and four at the opposite end. One nucleus from each group of four now moves to the center of the macrogametophyte; and cell division occurs, the macrogametophyte being divided to form seven cells (Fig. 344, *E*). At each end are now three cells, each with a single nucleus; and in the central part is a large cell containing two nuclei. The cells at the micropylar end of the

macrogametophyte are the *egg* and two *synergids;* at the opposite end are three *antipodal cells;* and the large two-nucleate cell is the *primary endosperm cell.*

From this history of macrospores and macrogametophyte there are, among the 150,000 or more known species of angiosperms, many variations. One of the more striking of these variations is found in the evening primroses, in which the mature macrogametophyte contains but four nuclei and three cells, instead of eight nuclei and seven cells. Another variant condition occurs in species of *Peperomia,* belonging to the pepper family; here the macrogametophyte has sixteen instead of eight nuclei; the number of cells varies with the species.

331. Microgametophyte. The development of a microspore into a microgametophyte begins while the microspore is still within the pollen sac. The microspore divides to form a relatively large *tube cell* and a smaller *generative cell* (Fig. 345, *B*). Since a prothallial cell is usually not produced, the history of an angiosperm microgametophyte is shortened as compared with that of a microgametophyte of a gymnosperm. In most angiosperms the two-celled microgametophyte (now a *pollen grain*) is liberated, and by the aid of winds, insects, or other agencies it may be carried to the stigma of the same or of another flower.

After the pollen grain lodges on a stigma, the tube cell grows out as a pollen tube (Fig. 345, *C–E*). The tube elongates rapidly, growing through the style to the ovary, and finally to an ovule. In some plants the pollen tube may grow from stigma to ovule within a few hours. In the bean, for example, this growth requires eight to nine hours. The nucleus of the tube cell is located at this time a short distance from the growing end of the tube. The generative nucleus divides into two *male gamete nuclei.* In some cases this nuclear division is followed by a division of the generative cell into two *male gametes;* in some angiosperms, however, the *cell* division is apparently omitted. The division of the generative nucleus, whether or not it is followed by a division of the generative cell, occurs in some species within the pollen grain before the latter is liberated from the pollen sac; but more commonly this division occurs after the beginning of the growth of the pollen tube. In either case, the male gametes or gamete nuclei move down the pollen tube and come to lie a short distance behind the tube nucleus. When a pollen tube reaches an ovule, it usually grows

through the micropyle to the nucellus, through the nucellus, and into the micropylar end of the macrogametophyte.

332. Pollination. Pollination in most angiosperms is brought about by winds or by insects. Wind-pollinated species are chiefly those that grow in localities exposed to the wind, or those which grow close together in large numbers. Among the smaller angiosperms the grasses, which form extensive stands of one or a few species, as in meadows where the wind has a free sweep, are largely wind-pollinated. Many trees, whose flowers are high above the ground and are thus exposed to the wind, also are wind-pollinated. Wind-pollinated flowers produce relatively large amounts of pollen and have large, and frequently rough or hairy, stigmas on which pollen grains may lodge.

Insect pollination has certain advantages over wind pollination. It is more economical because the pollen-carrying insect commonly travels from flower to flower of the same species. Consequently, a particular pollen grain has a better chance of reaching a stigma, and it is

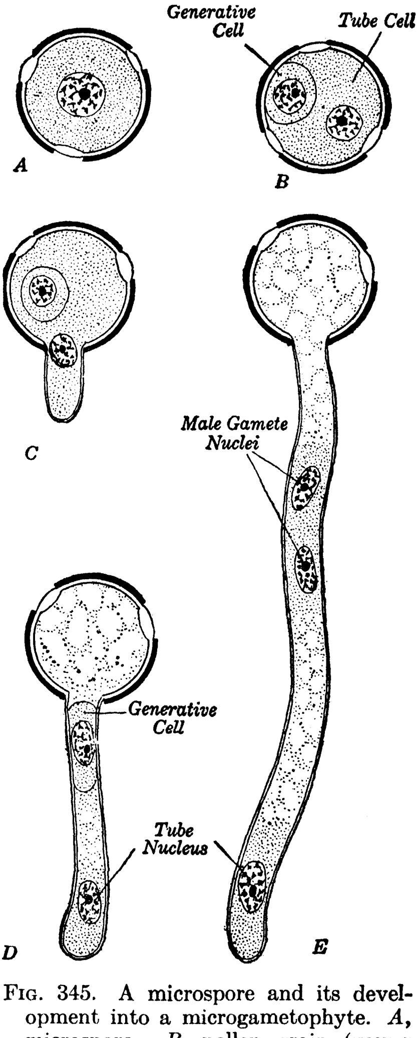


FIG. 345. A microspore and its development into a microgametophyte. *A*, microspore. *B*, pollen grain (young microgametophyte); the microspore has divided into a generative and a tube cell. *C*, "germination" of a pollen grain; development of a pollen tube. *D*, the generative cell has moved into the pollen tube. *E*, the generative nucleus has divided into 2 male gamete nuclei. All figures diagrammatic.

unnecessary for the plant to produce such enormous amounts of pollen as characterize wind-pollinated plants. Insect pollination is a method especially suitable for those species whose individual plants are more or less isolated. Another advantage is the greater opportunity offered for cross-pollination.

Insects visit flowers to gather food, or in special cases to deposit their eggs. Certain insects, including many moths, gather nectar only; others, such as bees, collect and utilize as food both nectar and pollen. The structure of a flower is often such that, when an insect visits it, portions of the insect's body become dusted with pollen which may rub off against the stigma of the next flower visited. The relations of their flowers to insects have apparently been an important factor in the evolution of angiosperms; and one reason why angiosperms as a group have been so successful is the fact that many of them have secured the help of insects in pollination. The relations of insects to flowers have likewise been an important factor in the evolution of insects. These statements imply, not that the advantage of a particular structure of a flower or of an insect has been the cause of the appearance of that structure; but rather that, when a particular structure has once appeared and has proved useful, it has persisted. Hence the present great variety in form and structure among both flowers and insects may be in part accounted for by the interrelations between insects and angiosperms, especially in respect to pollination.

Salvia (Fig. 346) illustrates a rather high degree of structural correlation between flower and insect. The corolla of Salvia is tubular below; its upper portion is divided into two lips. The lower lip of the corolla serves as a landing-stage for insects visiting the flower; the upper lip constitutes a protective shield for the stamens and stigma. There are two stamens. The basal part of each filament is fixed; jointed to the upper end of this short basal part is a curved lever whose two arms are unequal in length. The shorter arm is sterile; the longer arm bears an anther and extends within the curved upper lip of the corolla. When a bee alights upon the lower lip and attempts to thrust its nectar-collecting appendages into the corolla tube, its head presses against the short arm of the lever. When this sterile arm is depressed, the basal part of the filament serving as a fulcrum, the longer arm swings into contact with the hairy surface of the back of the insect. If the

pollen in the anther is mature, it is dusted upon the bee's body. Smaller insects attempting to secure nectar are not strong enough to depress the short arm of the lever. In a young flower of Salvia, the style lies within the concavity of the upper corolla lip. As the flower matures, the style elongates and curves so that the stigma is midway between the upper and lower lips of the corolla. If a bee sprinkled with pollen visits such a flower in search of nectar, its pollen-dusted back rubs against the stigma and there deposits some of the pollen.

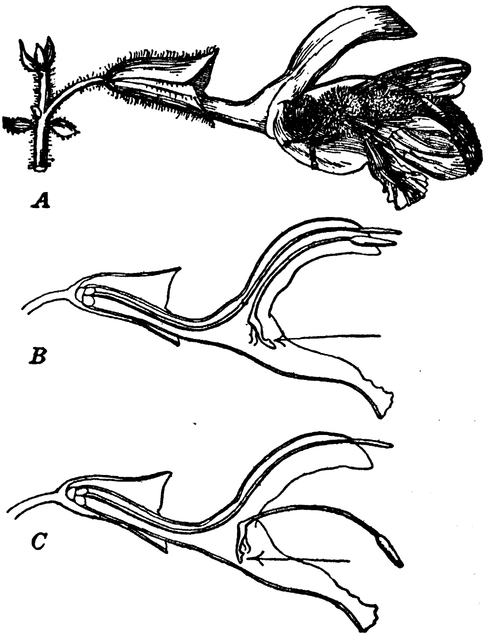


Fig. 346. Pollination of Salvia. *A*, flower into which a bee has entered. *B*, *C*, lengthwise sections of a flower before and after the bee enters, showing the effect of its entrance upon the position of a stamen; arrows indicate the direction taken by the bee. After Kerner.

333. Gametic Union. As the tip of a pollen tube enters a macrogametophyte, it enlarges somewhat, its end bursts, and some of its contents, including the male gamete nuclei, are discharged into the macrogametophyte (Fig. 347). One male nucleus enters the egg and unites with its nucleus, so forming a zygote with 2 n chromosomes. The other male nucleus passes to the primary endosperm cell and unites with the two nuclei of that cell; sometimes these two nuclei have united before the male nucleus reaches them. The union of three nuclei in the primary endosperm cell is a feature peculiar to the angiosperms. Since these nuclei are gametophytic, the nucleus formed by their union contains 3 n chromosomes. On the basis of its chromosome number, therefore, the primary endosperm cell, after this union of three nuclei, is neither gametophytic (with n chromosomes) nor sporophytic (with 2 n chromosomes).

334. Development of a Seed. Just as in a gymnosperm, the structure from which the seed of an angiosperm is matured (the ovule) is well along in its development at the time of gametic union. As in a gymnosperm, also, the zygote of an angiosperm develops into the embryo of the mature seed, and the integument (or integuments) mature into the seed coat (or coats). Differently from the condition in gymnosperms, the macrogametophyte

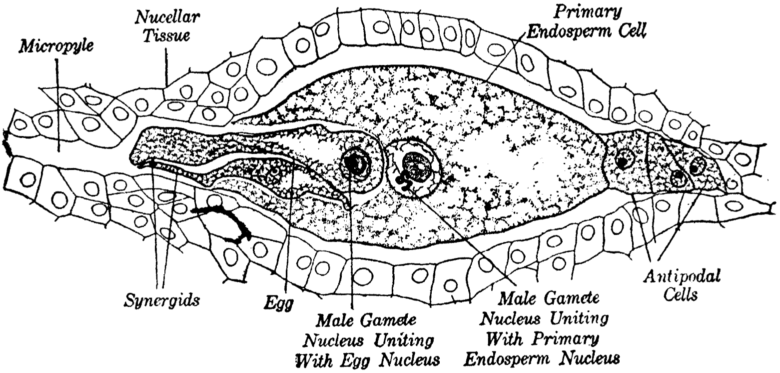


FIG. 347. Mature macrogametophyte of prickly lettuce. One male gamete nucleus is uniting with the egg nucleus, 1 with the primary endosperm nucleus (the latter previously formed by a union of 2 nuclei). Drawing by K. L. Mahony.

(the n-chromosome generation) does not persist as a tissue in which most of the reserve food is stored. Instead, the primary endosperm cell, now containing, as has just been seen, a nucleus with 3 n chromosomes, develops into a temporary or permanent tissue of the maturing seed. The development of a seed shows considerable variation in different angiosperms, although certain features of this development are common to all species.

The shepherd's purse (*Capsella*) represents a type of seed-development commonly found in dicotyledons. Before the gametes unite, the ovule of Capsella contains an elongated, somewhat crescent-shaped seven-celled macrogametophyte within a thin nucellus (macrosporangium), which in turn is surrounded by two integuments. Shortly after gametic union the ovule grows rapidly, its growth being due mainly to an extraordinary increase in size of the primary endosperm cell. This enlargement of the primary endosperm cell involves the development of a large central vacuole, the dense cytoplasm thus being limited to a peripheral

layer which is thickest in the regions at the ends of the cell. As a result of the division of the primary endosperm nucleus and of the repeated division of nuclei derived from it, the cell finally contains many nuclei, each with 3 *n* chromosomes, which are fairly evenly distributed throughout the dense cytoplasm (Fig. 348). Considerably later, by cell division, this large many-nucleate cell becomes a many-celled endosperm.

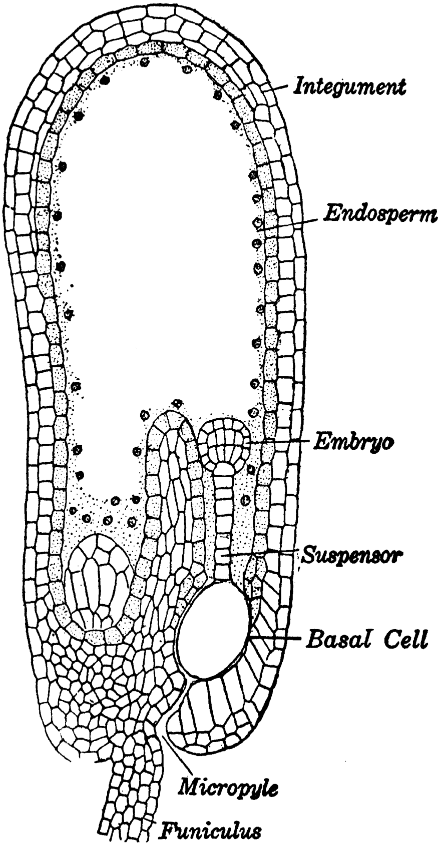


FIG. 348. Capsella; an immature seed containing a young embryo.

This tissue should not be confused with the endosperm of a gymnosperm, which is the macrogametophyte and each of whose cells has *n* chromosomes. The endosperm of an angiosperm is a new structure developed after gametic union, whose cells are ordinarily marked by the presence of 3 *n* chromosomes. Despite these differences, the endosperm has the same function in both gymnosperms and angiosperms—that of providing for the nutrition of the young sporophyte.

The endosperm of Capsella is in time almost entirely digested and absorbed by the developing embryo. In some angiosperms, the endosperm persists to form a relatively large portion of the mature seed; in these cases the endosperm constitutes a tissue filled with reserve foods which will be used by the embryo during the germination of the seed.

While the endosperm is being formed, the zygote of Capsella develops into a many-celled structure, the *embryo* or young sporo-

phyte. The development of the embryo begins with the division of the zygote and of its daughter cells to form a short, few-celled filament (Fig. 349, *A*). The cell of this filament farthest from the micropyle is the one which will form most of the body of the embryo; the other cells of the filament constitute a *suspensor* whose

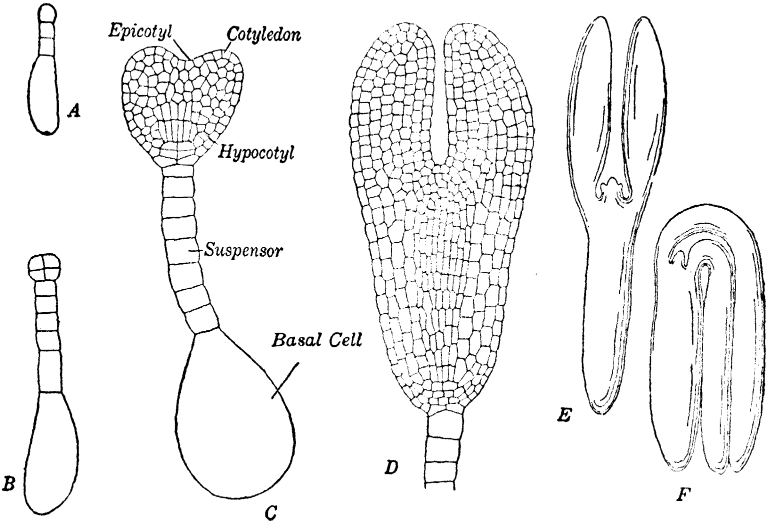


FIG. 349. Development of an embryo of Capsella. *A*, *B*, early stages. *C*, *D*, later stages, showing the differentiation of hypocotyl and cotyledons. *E*, *F*, other embryos of the dicotyledonous type.

growth pushes the terminal cell toward the center of the primary endosperm cell. The suspensor is never more than a few cells in length; its basal cell is always larger than its other cells and is imbedded in the micropylar end of the nucellus. The terminal cell of the filament gives rise by divisions to two tiers of four cells each (Fig. 349, *B*). It is at this stage that differentiation of the parts of the embryo takes place—the tier of four cells nearer the suspensor by repeated division and growth developing into the major portion of the *hypocotyl*, the four cells farther from the suspensor similarly forming the *cotyledons* and *epicotyl*.

In the terminal portion of the developing hypocotyl the differentiation of tissue regions occurs that is characteristic of a root tip. A root cap which covers, and is continuous with, the end of the hypocotyl is formed from the adjacent cells of the suspensor.

The group of cells from which the cotyledons and epicotyl are to develop is for a time a hemispherical mass. At a later stage, cell division and growth go on most rapidly at two points near the apex of this mass. As a result, two projections appear which are the primordia of the cotyledons (Fig. 349, *C*). The apex of the cell mass between the young cotyledons remains substantially unchanged for a considerable time. Later, however, when the cotyledons have become comparatively large, cell division and growth are resumed at this point, and so a small projection, the epicotyl, later to produce most of the aërial portion of the plant, is formed between the bases of the cotyledons. When young, the two cotyledons are widely divergent; as the development of the embryo continues they become more nearly parallel; still later, inequalities of growth on their respective sides cause both cotyledons to fold over on one side of the embryo, and to grow parallel to the hypocotyl (Fig. 349, *F*).

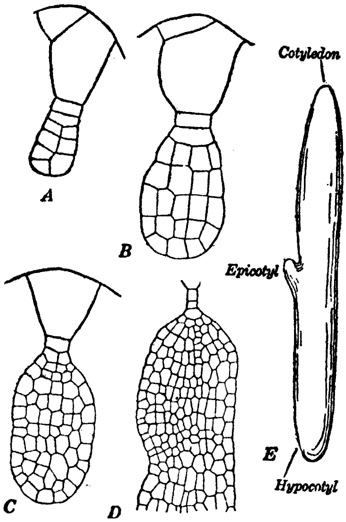


FIG. 350. Development of a monocotyledonous embryo (Sagittaria). *A–D*, early stages; redrawn from Schaffner. *E*, mature embryo.

During the later stages in the development of the embryo, its cells, particularly those of the cotyledons, become filled with reserve foods. In some dicotyledons, such as the bean, the cotyledons become conspicuously enlarged.

A type of embryonic development characteristic of many monocotyledons is found in the arrow-head (*Sagittaria*, Fig. 350). Here the zygote develops into a row of three cells, the basal one of which is much the largest and does not divide; the median cell by division and growth develops into a suspensor, a hypocotyl, and a *lateral* epicotyl; and the terminal cell into a *single* terminal cotyledon.

During the development of most angiosperm seeds, while the endosperm and embryo are growing, the nucellus, antipodal cells, and synergids disappear, and the integument or integuments become modified to form the protective seed coat or coats. All these

changes by means of which an ovule and its inclusions develop into a seed take place within the ovary.

335. Fruits. Angiosperms differ from gymnosperms in the development of a carpel (macrosporophyll) or carpels into a pistil whose lower portion, the ovary, encloses the ovules. Another

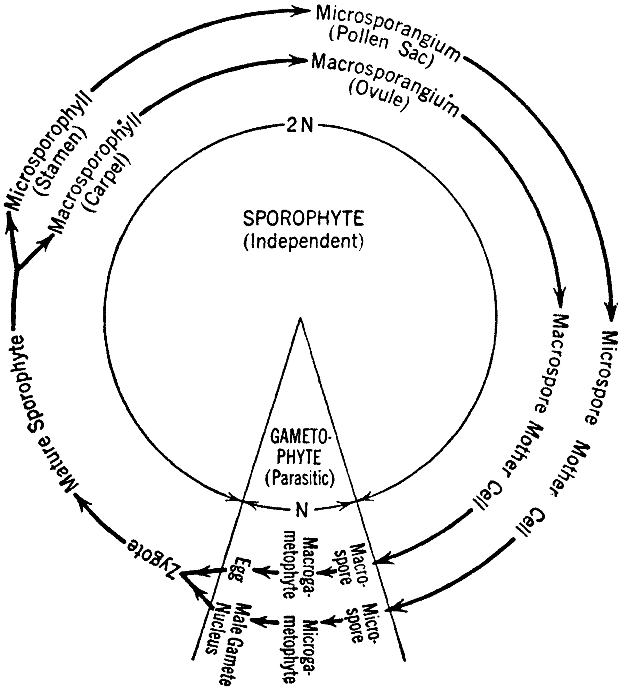


Fig. 351. Life cycle of an angiosperm.

feature peculiar to the angiosperms is the development of the ovary and its contents into a *fruit.*

Pollination and gametic union influence the subsequent development both of the ovules and of the ovary enclosing the ovules. Maturation of the tissues of the ovary into a mature fruit may or may not involve a very considerable increase in size. The different parts of the ovary in different species mature into tissues and structures of varied nature. Different angiosperms, therefore, display great variation in the size, form, and structure of their mature fruits. Development of a fruit often involves other parts of the flower than the ovary, such as the sepals and the receptacle. A

true fruit, however, includes only structures derived from the ovary.

When fruit and seed are mature the seed is shed, either separately or still enclosed by the fruit. Under appropriate conditions the seed may germinate and the embryo resume development into a mature sporophyte.

336. Classes of Angiosperms. Angiosperms are divided into two classes, *dicotyledons* and *monocotyledons.* These classes are named from the numbers of cotyledons which respectively characterize their embryos; the embryo of a dicotyledon (such as Capsella) having ordinarily two cotyledons, that of a monocotyledon (such as Sagittaria) ordinarily only one. Attention has already been called (Chaps. IV–VII) to certain characteristic differences between these two classes in the structure of the plant body (the sporophyte). These and other features which chiefly distinguish dicotyledons and monocotyledons may be summarized as follows:

(*a*) The embryo of a dicotyledon has typically a terminal epicotyl and two lateral cotyledons; the embryo of a monocotyledon has typically a lateral epicotyl and a single terminal cotyledon.

(*b*) Most dicotyledonous stems are characterized by the presence of a single cylinder of vascular bundles; in most monocotyledonous stems the bundles are scattered throughout the stele.

(*c*) Each vascular bundle in a dicotyledonous stem possesses a cambium; that of a monocotyledonous stem lacks a cambium.

(*d*) A dicotyledonous root has, as a rule, but few ridges radiating from the central mass of primary xylem; a monocotyledonous root usually has numerous xylem ridges.

(*e*) A dicotyledonous root develops a cambium; a monocotyledonous root rarely forms one.

(*f*) The leaves of dicotyledons are netted-veined; those of monocotyledons are usually parallel-veined.

(*g*) The parts of a dicotyledonous flower (sepals, petals, stamens, and carpels) are very commonly in fours or fives or in multiples of four or five; in monocotyledons, the floral parts commonly occur in threes or in multiples of three.

There is no characteristic difference between dicotyledons as a class and monocotyledons as a class in the structure or the development of the gametophytes.

337. Angiosperms and Gymnosperms. Angiosperms (including dicotyledons and monocotyledons) and gymnosperms are alike in

the essential points that distinguish the seed plants from plants below them in the evolutionary scale. Angiosperms, however, differ from gymnosperms in the following respects:

(*a*) In the presence of sepals, petals, or both, in addition to sporophylls.

(*b*) In the development of the macrosporophyll or macrosporophylls into a pistil.

(*c*) In some further reduction of the microgametophyte.

(*d*) In the lodging of the young microgametophyte (pollen grain) on the stigma at some distance from the macrosporangium.

(*e*) In a marked reduction of the macrogametophyte to a few-celled structure.

(*f*) In the functioning of a male gamete in initiating the development of the endosperm.

(*g*) In the development of a fruit.

(*h*) Typically, in the presence of vessels in the xylem.

338. Progress from Bryophytes to Angiosperms. In the evolutionary series leading from bryophytes through pteridophytes to seed plants, there has been no modification of the most fundamental features of the life cycle. Throughout this series the gametes unite to form a zygote that develops into a sporophyte whose distinctive function is the production of spores. A spore, in turn, develops into a gametophyte whose distinctive function is the production of gametes. Throughout the entire series, also, the chromosome number is doubled when gametes unite, and halved when spores are formed.

Despite these basic similarities, however, the series from bryophytes to seed plants displays certain evolutionary tendencies that culminate in the angiosperms.

(*a*) The gametophyte of a bryophyte is the larger, independent generation; in a fern it is small but still independent; in Selaginella and a few other pteridophytes it is much reduced and essentially parasitic upon the sporophyte; in seed plants it is still more reduced and entirely parasitic, reaching the extreme in these respects in angiosperms. The sporophyte has followed the opposite evolutionary course; small and largely parasitic in bryophytes, in ferns it is the larger generation, parasitic only in an embryonic stage; in

Selaginella it is but briefly parasitic upon the very small macrogametophyte; in gymnosperms the same is true; but in angiosperms the nutritive function of the macrogametophyte has been transferred to a new 3 n-chromosome structure, the endosperm. In addition, in both gymnosperms and angiosperms the old sporophyte has become partially responsible for nourishment and protection of the young sporophyte.

(*b*) In bryophytes and pteridophytes gametic union depends upon the presence of water to enable male gametes to reach the eggs. In seed plants the male gametophyte has developed a new structure, the pollen tube, which insures the transport of male gametes to the neighborhood of an egg. Male gametes, still motile in the more primitive gymnosperms such as Zamia, in most gymnosperms and in angiosperms have lost their flagella and much of their independent motility, depending upon the pollen tube to supply a pathway to the female gametophyte.

(*c*) In bryophytes and most pteridophytes all spores are substantially alike in size. In certain bryophytes spores are sexually differentiated in the sense that some are destined to give rise to male, some to female, gametophytes. This is not the case, however, in many bryophytes or in most ferns. In Selaginella and a few other pteridophytes, spores are of two distinct sorts: large (female) and small (male). Sexual differentiation in Selaginella does not, however, begin with the spores; it has been pushed back to the sporangia, structures of the sporophyte. Although the sporangia are asexual reproductive structures, they are sexually differentiated. In gymnosperms sexual differentiation extends back to the sporophylls and strobili. In angiosperms with separate pistillate and staminate flowers this differentiation affects all the structures of the flower; and in some angiosperms with separate pistillate and staminate plants the whole sporophyte is sexually differentiated.

(*d*) In most bryophytes and pteridophytes a spore develops into a gametophyte after it has left the sporangium. In some species of Selaginella the production of two kinds of spores is correlated with the fact that a spore of the larger type develops into a macrogametophyte entirely within the macrosporangium. Shortly after gametic union the macrogametophyte is liberated. In a gymnosperm the macrogametophyte is not similarly liberated. Consequently, during its early development the sporophyte of a gymno-

sperm is surrounded both by the macrogametophyte and by structures of the old sporophyte.

Permanent retention of macrogametophyte within sporangium, the beginning of the development of the zygote into a new sporophyte while still enclosed within both structures, and the maturation of the integument, or of nucellus and integument, into protective tissues mark the appearance of a wholly new structure—the seed. Another novel feature connected with seed-development is the temporary cessation of growth of the new sporophyte at a certain stage. The seed of an angiosperm shows a further advance in that the macrogametophytic tissue is obliterated after gametic union, reserve foods for the young sporophyte being stored in a newly developed tissue, the endosperm, or in the young sporophyte itself.

CHAPTER XXX

SEEDS AND FRUITS

339. Nature of Seeds. A seed is a matured ovule. During its maturation, the zygote develops into an *embryo*, the primary endosperm cell into a nutritive tissue (the *endosperm*); and the integument or integuments develop into a *seed coat* or seed coats. Development of the embryo is initiated by the union of a male nucleus with the egg nucleus; that of the endosperm, by the union of a male nucleus with the two nuclei of the primary endosperm cell. Development of an integument into a seed coat is a secondary phenomenon resulting from a stimulus arising in the developing embryo, endosperm, or both. The endosperm may persist in the seed, or it may be absorbed by the developing embryo. In the seeds of a few plants a portion of the nucellus persists as a food-storage tissue.

Seeds of angiosperms differ widely in structural details. The two classes of angiosperms, dicotyledons and monocotyledons, are named from a striking difference between their respective seeds. The embryo of a dicotyledon has two approximately equal, laterally placed cotyledons, between which is a terminal epicotyl; the embryo of a monocotyledon typically has one large cotyledon, apparently borne terminally, and a laterally placed epicotyl. Many angiosperm seeds, such as those of corn, contain a considerable amount of endosperm when mature. In the development of the seeds of other angiosperms, such as the shepherd's purse and bean, the endosperm, although formed, is quickly absorbed, and reserve foods are stored in the cotyledons instead of in an endosperm. In general the mature seed of a monocotyledon contains an endosperm; the mature seeds of some dicotyledons possess endosperms, those of others do not.

340. Structure of Seeds. On the concave edge or face of a bean seed (Fig. 352) is a fairly large scar, the *hilum*, marking the former point of attachment of the seed to the short stalk (funiculus) which connected the ovule with the edge of the carpel. Near one end of the hilum is the micropyle. There are two seed coats de-

veloped respectively from the two integuments, the inner coat being somewhat thicker and heavier than the outer, and the two more or less firmly united. The embryo occupies all the space within the seed coats. It has two large, thick, firm cotyledons, closely appressed and enclosing the epicotyl which bears two opposite overlapping immature foliage leaves. The hypocotyl lies outside the cotyledons and is bent backward along the line of

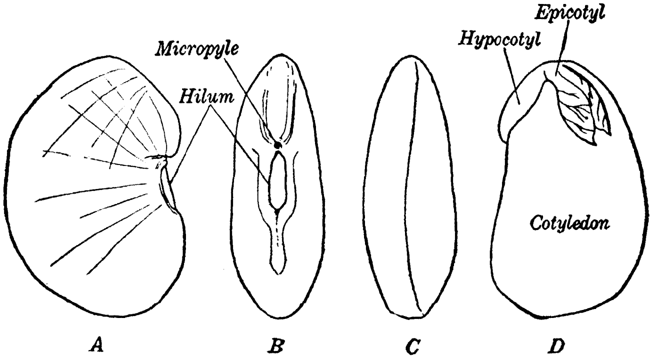


FIG. 352. Seed of bean. *A*, side view. *B*, as seen from the inner (attached) edge. *C*, from the outer edge. *D*, embryo; seed coats and 1 cotyledon removed.

meeting of the cotyledons on the concave edge of the seed. The cotyledons contain large reserves of starch and proteins, as well as some sugars and fats.

A seed of a lily is broad and flat. Its seed coats are thin and membranous, sometimes forming a narrow, wing-like expansion about the entire circumference of the seed. Within the seed coats is a firm, starchy endosperm, in whose center the relatively small embryo is imbedded (compare the iris seed, Fig. 353). The embryo is long and narrow, nearly cylindrical, and slightly curved. The hypocotyl is near the micropylar end of the seed and frequently projects a short way beyond the surrounding endosperm. There is a long, massive cotyledon, partly surrounding a small epicotyl. The embryo contains some fats and proteins. The endosperm is rich in starch.

341. Power of Seeds to Germinate. One great difference between a seed and most other plant organs, such as root, stem, or leaf, is that in the seed the processes characteristic of living matter may go on very slowly. Dormant seeds respire, but res-

piration in an air-dry seed is almost infinitesimal in amount as compared with respiration in a germinating seed or in a stem or leaf. The partial suspension of activity in a seed results primarily from its comparative dryness. During the maturing of a seed the greater part of its contained water has been lost. In most cases the seed coat is relatively impermeable to both water and oxygen, so that no new supply of water can enter. Although the

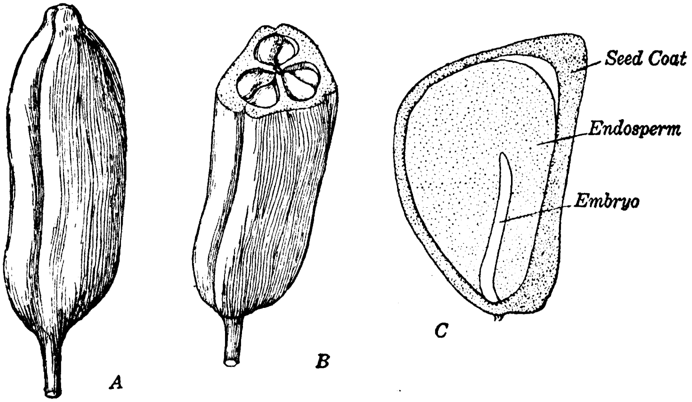


FIG. 353. *A*, *B*, surface view and cross section of a fruit of iris. *C*, lengthwise section of an iris seed.

amount of water in seeds is usually small, some water must be present if the embryo is to survive, and this small amount of water is tenaciously held.

It is commonly said that a seed is *ripe* at its separation from the parent plant, but this ripeness is not necessarily coincident with a readiness to germinate. Many seeds germinate at maturity or shortly thereafter if conditions are suitable. This is especially true of short-lived plants, including many crop plants, whose seeds usually germinate as soon as they are scattered. Such power of early germination is sometimes a disadvantage; in warm, moist autumns, for example, the seeds of corn may germinate while still upon the ear.

However, many seeds must undergo *after-ripening* before germination can occur. Among other things, after-ripening involves changes in the acidity of the seed contents, the formation of enzymes, and the digestion of stored foods. In some seeds these changes require days; in others, weeks, months, and even years are necessary. In certain cases the prolonged postponement of

germination is due to the hardness and thickness of the seed coats. Variations in permeability of seed coats may account for the fact that often some seeds germinate long before others of the same species. This latter condition, in annuals, insures the persistence of the species, even though a particular season proves unfavorable for germination.

The length of time during which seeds remain capable of germination varies greatly. At one extreme are those of willows and poplars, which must germinate within a few days or not at all. Some acorns will not germinate after a year; coffee beans, not after six months. Among common crop plants, tobacco has probably the longest-lived seeds; tobacco seeds 20 years of age have germinated. Seeds of certain species from dated herbarium collections have germinated after 87 to 130 years. The seeds of the pulse family, whose seed coats are notably impermeable to water and gases, are probably longest-lived, some retaining their vitality for 150 to 250 years. However, despite these extreme cases, no seeds can remain alive indefinitely. The stories told of seeds that germinated after being for thousands of years in Egyptian tombs are quite without foundation.

The ability of a seed to remain capable of germination depends both upon the structure of the seed coat and upon the nature of the substances within the seed. Seeds rich in enzymes quickly lose their power of germination. Those rich in fats do not survive as long as do those whose reserve foods consist largely of starch. A low water content, which reduces the rate of respiration and of other processes to a minimum, is responsible for the longevity of many seeds.

Although the presence of water is essential to germination, submergence in water for any great length of time results in the death of many seeds, including those of rye, oats, and corn. Seeds of not a few water plants, however, can withstand submergence for years, probably because of the extreme resistance offered by their seed coats to the penetration of water. If deeply buried in soil, many seeds retain the needed water and the power of germination almost indefinitely. Indian lotus seeds buried in the mud of Manchuria for 200 years have germinated after treatment with certain chemical substances which modified their permeability to water and gases. Many plants become weed pests because of the great longevity of their buried seeds.

342. Germination (Fig. 354). Germination depends upon certain external factors; of these the most important are the presence of water and of oxygen and a suitable temperature. Water is essential to the expansion of certain parts of a seed, as well as to the initiation of activities within, including the digestion of stored food and its translocation to the parts of the embryo where it is to be utilized. When a bean seed is planted, water does not enter at equal rates over the entire surface of the seed, but enters most readily through the region of the hilum. This fact is shown by a wrinkling of the seed coat first in the neighborhood of the hilum. The entrance of water results from an actual imbibition by the cell walls of the seed coat in the region of the hilum, followed by a transfer of the water by imbibition and osmosis into interior cells.

Temperature is an important factor, since up to a certain point the higher the temperature the more rapid are various processes within cells. Assimilation and respiration are much more active at 20° than at 5° C. Temperatures for the germination of most seeds range from 3° to 49° C., the optimum being about 33° C. The minimum temperature at which seeds will germinate varies greatly as between different species.

Light has no direct or indirect influence upon the germination of most seeds, although some are sensitive to light.

Oxygen is essential to the respiration of a developing seedling, both before and after it emerges from the seed coat. A germinating seed is the seat of a series of processes, all involving the expenditure of energy. Since the energy to be used in these processes must be released by respiration, and since, therefore, respiration is characteristically rapid in germinating seeds and seedlings, a considerable supply of oxygen is necessary.

When germination begins, the imbibition of water by the embryo and endosperm causes a swelling of these structures, which expands and finally ruptures the seed coat. In some cases the breaking of the seed coat is irregular, as in the bean; in others it takes place along definite lines. The seed coat of a germinating squash seed is broken first at its narrow end. The earliest growth of the embryo involves chiefly an enlargement of already existing cells as a result of the intake of water, rather than a formation of new cells by division. Growth is at first largely localized in the hypocotyl, which elongates and soon emerges from the seed coat. Seeds of many plants are so constituted that the part of the seed

containing the hypocotyl is that which is most likely to be turned toward the soil. For the majority of seeds, however, this is not the case, and it is a matter of chance whether the side of the seed from which the hypocotyl emerges is toward or away from the soil. In any case, the primary root, which constitutes the greater part of the hypocotyl, turns to whatever extent is necessary to enable it to grow downward. This bending is due to the strongly positive geotropism of the hypocotyl.

At least after the first stages of germination, the growth of the hypocotyl and of other parts of the embryo involves the formation of new cells by division as well as the enlargement of already existing cells. The formation and growth of new cells necessitate the use of foods. Since the seedling as yet has no chlorophyll-containing cells and hence can not carry on photosynthesis, it is dependent for the foods needed in its growth as well as for those utilized in respiration upon the reserves stored in the seed. If, as is frequently the case in dicotyledons, reserve foods are stored in the cotyledons, these foods are digested by enzymes produced in certain parts of the embryo. The digested foods are then translocated to the growing portions of the seedling where they are to be utilized. In seeds containing endosperm, the secretion of enzymes and the absorption of digested foods from the endosperm are brought about largely or entirely by the cotyledon or cotyledons. This is especially true of members of the grass family such as wheat and corn, in which the cotyledon is a digestive and absorptive organ that never emerges from the seed coat.

During its further growth the hypocotyl frequently becomes arched in such a way as to pull the cotyledons out of the seed coat. This arching is well illustrated in the seedlings of the common bean (Fig. 354, *A*). In the development of the seedlings of the squash and of some of its relatives, the removal of the cotyledons from the seed coat is assisted by a peg-like outgrowth from the hypocotyl (Fig. 354, *B*). Sometimes, as in the castor bean, the arching and elongation of the hypocotyl carry upward into the air the cotyledons, still enclosed by the seed coat; later the hypocotyl straightens, and the seed coats are removed in consequence of the growth of the cotyledons themselves. The arching of the hypocotyl and its later straightening result from a negative rather than a positive geotropism of the portion of the hypocotyl in the vicinity of the cotyledons. Sometimes, as in the pea and the scarlet runner bean,

the hypocotyl remains short and unarched; the cotyledons, like the single cotyledon of the corn, never emerge from the seed coat, and the shoot which issues above ground and produces foliage leaves is developed entirely from the epicotyl.

In those cases in which the cotyledons are withdrawn from the seed coat and pushed above the soil, they form more or less chlorophyll and to some extent function as foliage leaves. Often, however, as in the common bean, the cotyledons are thick and soon shrivel

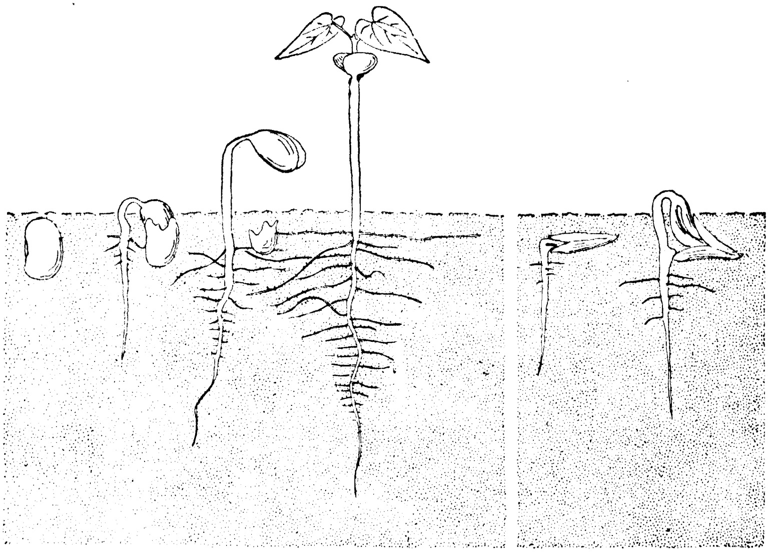


FIG. 354. *A*, stages in the germination of a bean seed. *B*, germinating seed of squash; the emergence of the embryo from the seed coat is assisted by a peg-like outgrowth of the hypocotyl.

and are dropped off. Cotyledons of other seedlings, such as those of the castor bean, become flat, expanded leaves which persist and function for some time in photosynthesis. As a rule, however, cotyledons are different in form from the leaves developed by the epicotyl, often being smaller and simpler.

If the cotyledons emerge from the seed, the epicotyl is brought out with them. If, as in the corn and the pea, the cotyledon or cotyledons do not emerge, the epicotyl is the last part of the embryo to be freed from the seed coat. When the epicotyl emerges, its structures, which are to develop into all or nearly all the aërial

parts of the plant, are in a very immature state. The stored foods in the seed must therefore be chiefly relied upon by the seedling until the stem and its leaves have developed sufficiently to make the plant independent.

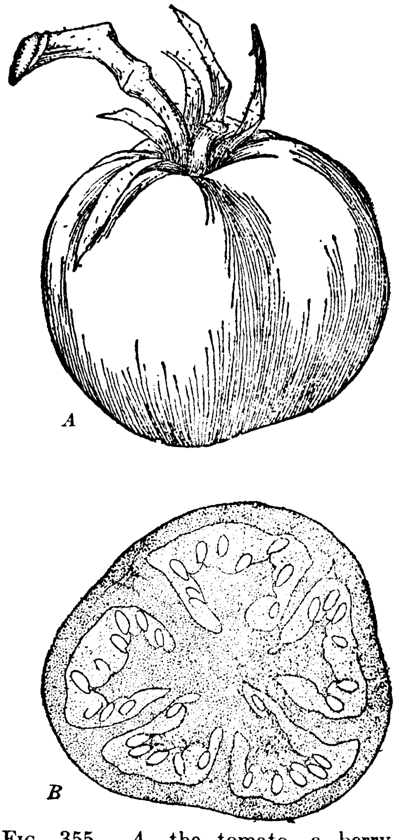


FIG. 355. *A*, the tomato, a berry whose ovary wall has become greatly thickened and juicy. *B*, the same in cross section. The fruit here shown was developed from 5 carpels.

343. True and False Fruits. The changes by which an ovule and its inclusions develop into a seed within an ovary are accompanied by a metamorphosis of the ovary into a fruit. A *true fruit*, in the strict interpretation of the term, is a structure developed solely from an ovary containing one or more seeds. Often, however, the development of a fruit involves parts of the flower other than the ovary, such as the sepals, the receptacle, and the floral axis. A structure of this nature, not derived in its entirety from the ovary, is called a *false fruit.* The apple is a false fruit, since its fleshy portion is derived mainly from the receptacle.

344. Simple Fruits. When but a single ovary, with or without surrounding structures, develops into a fruit, whether true or false, the fruit is simple. At the time of pollination and of gametic union the ovary walls of all species are essentially alike in that they consist of tissues which, except for vascular bundles and provascular strands, are homogeneous in structure. The growth and maturation of the ovary wall after pollination result, however, in the development of fruits which differ markedly with respect to the tissues that compose them. Simple fruits are either fleshy or dry.

345. Fleshy Fruits. If the fruit into which an ovary matures is one in which the ovary wall (at least its inner portions) and the interior structures of the ovary are enlarged and juicy, the fruit is a *berry*. The seeds, each with a hard coat of its own, are imbedded in the juicy flesh of the fruit. A berry may develop from an ovary composed either of a single carpel or of more than one carpel. The tomato, orange, and grape are berries. The tomato (Fig. 355) is a large berry consisting in primitive forms of two carpels, although in many cultivated varieties there are twelve or more. The fleshy portion of the fruit is developed from the ovary wall, the very greatly enlarged ovule-bearing ridges, and the partitions between the carpels. Citrus fruits, including orange, lemon, and grapefruit,

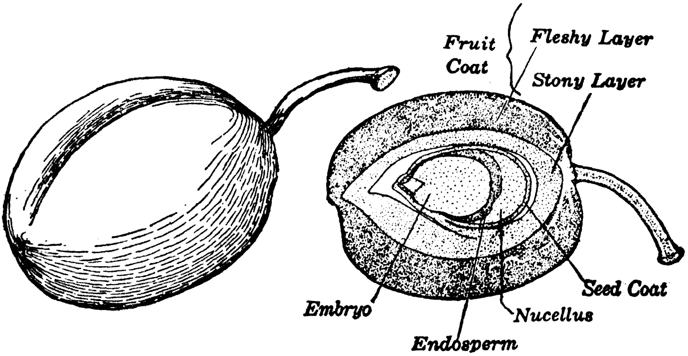


FIG. 356. The plum, a stone fruit (immature).

are berries of a type with a tough, leathery rind. Each section of an orange or of a grapefruit represents a carpel, the carpels being firmly attached to one another at their outer surfaces but readily separable along their lateral faces. Except for the space occupied by the seeds, each carpel is filled with many small hair-like outgrowths arising from its inner surface. As the fruit matures, these outgrowths become filled with juice. The date is a berry with a single hard seed, the fleshy part having developed from the ovary wall.

Several false fruits also are classified as berries. The currant and gooseberry are of this sort. The fleshy part of each of these fruits is developed largely from the receptacle. In a blueberry or cranberry the calyx tube forms a part of the juicy portion of the fruit. A banana is a berry whose "peel" has been developed from

the receptacle. Melons and squashes are false fruits of the berry type. In these, the receptacle is closely united with the ovary wall.

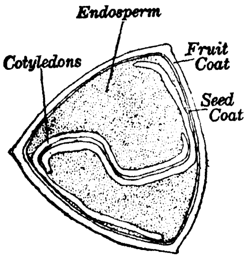


FIG. 357. Cross section of a fruit of buckwheat.

In a stone fruit (*drupe*), such as a plum (Fig. 356), peach, or cherry, the outermost layers of the ovary wall form the skin; the layers next within become fleshy or fibrous; and the innermost layers, becoming hard and stony, form the "pit" which encloses the comparatively soft, thin-coated seed. The walnut and coconut are stone fruits, the hard shell of the so-called "nut" in each case being formed from the inner layer of the ovary wall.

During the maturation of the apple type of fruit (*pome*), the petals and stamens wither and fall away; the upper portion of the style withers also but may remain attached. In the apple the carpels are more or less firmly united with one another, at least at their inner edges, and are completely surrounded by, and united with, the receptacle. The outer portion of the ovary wall constitutes part of the pulp of the apple; the inner part of the ovary wall is leathery, and each division of the core, corresponding to one carpel, usually contains two, sometimes more, seeds. The greater part of the fleshy tissue is developed from the receptacle. The sepals frequently remain attached at the upper end of the mature fruit.

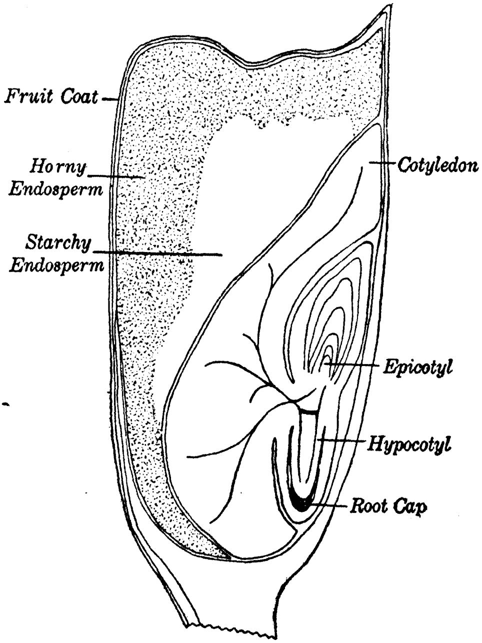


FIG. 358. Lengthwise section of a fruit (grain) of corn.

346. Dry Fruits. Instead of becoming fleshy, an ovary may mature into a dry, more or less hard fruit. There are two general types of dry fruits: *indehiscent* fruits which do not split open at maturity, and *dehiscent* fruits which regularly split at maturity and expose the contained seed or seeds. As a general rule, an indehiscent dry fruit contains a single seed and a dehiscent dry fruit contains more than one seed.

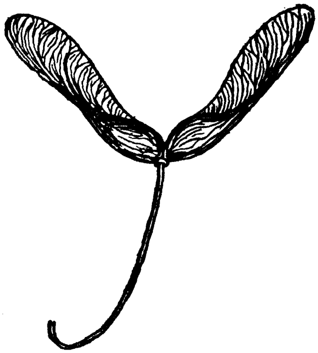


FIG. 359. Fruits (samaras) of maple.

If an indehiscent dry fruit contains but one seed, the seed being attached to the fruit wall at only one point, the fruit is an *achene.* Achenes are produced by the buckwheat (Fig. 357), sunflower, and buttercup. Since the fruit wall of an achene is merely a thin, dry layer enclosing the seed, the fruit is seed-like in appearance. The achenes of many plants are commonly called "seeds."

If the thin, transparent fruit wall is attached at all points to the seed coat, the dry fruit is a *grain.* Fruits of this type are produced by many members of the grass family, including the corn (Fig. 358), wheat, and other cereals. In a corn grain an abundant endosperm completely fills the seed coat except for the space at one side that is occupied by the embryo. The greater part of the embryo consists of a broad cotyledon whose infolded edges almost completely enclose the epicotyl. The small epicotyl bears several immature leaves, the oldest one of which constitutes a sheath that encloses the younger leaves and the epicotyl. Extending in a direction opposite to that taken by the epicotyl is a small hypocotyl, surrounded by a special sheath and partly surrounded by the large cotyledon. The endosperm consists of an opaque starchy and a translucent horny portion, the latter containing the major part of the protein foods. The embryo contains reserves of fats, sugars, some proteins, and small amounts of starch.

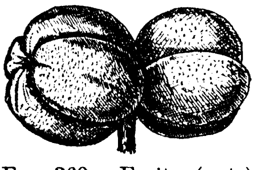


FIG. 360. Fruits (nuts) of hickory, each containing 1 seed.

In some cases the margin or the apex of an indehiscent dry fruit develops into a wing-like structure. A fruit of this type is known

as a *samara* (Fig. 359). The maple, ash, and elm bear samaras. In the flower of a maple two ovaries are borne side by side, a compound style arising at the midpoint of the upper edge. The outer upper angle of each ovary is extended and flattened into a wing. After the union of gametes, the ovaries enlarge greatly and the wings grow in length and breadth, finally becoming dry and papery.

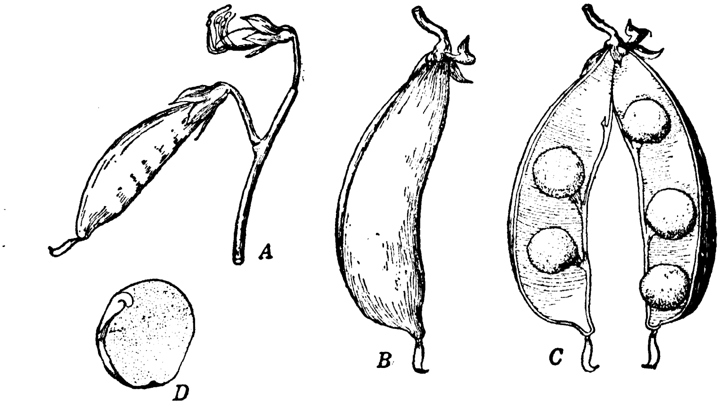


FIG. 361. Fruit (legume) and embryo of pea. *A*, immature fruits. *B*, surface view of a mature fruit. *C*, mature fruit split open. *D*, embryo, with 1 cotyledon removed.

The two ovaries (now fruits) fall from the tree still attached to each other, or they may split apart and fall separately.

A *nut* is similar in structure to an achene, but it is of larger size and it frequently develops from an ovary containing more than one ovule. In the latter case, only one ovule matures into a seed. In nuts, as in the hickory nut (Fig. 360), chestnut, hazelnut, or acorn, the shell is the fruit coat and the softer edible portion within is the seed. Some structures commonly known as "nuts" are something less than the whole fruit. An almond corresponds to the stone of a drupe, the outer fibrous part of its fruit coat having dried and fallen off. A coconut resembles an almond in that the hard shell is the inner part of the fruit coat. Some true seeds are also commonly called "nuts." A Brazil nut is a seed, 18 to 24 such seeds being borne in a single fruit. A horse-chestnut is also a seed; the fruit, a prickly capsule, contains 1 to 3 seeds.

A compound pistil, each carpel enclosing a single ovule, may mature into an indehiscent fruit whose parts (the carpels) separate from one another at maturity. The fruits of mallow and geranium

and of members of the parsley family are examples of this type, the *schizocarp.*

Dehiscent dry fruits may be developed from either simple or compound pistils. One type of dehiscent dry fruit is the *legume,* characteristic of the bean, pea (Fig. 361), and other members of the pulse family. A legume develops from a pistil consisting of a single carpel whose edges are united. Seeds are borne attached alternately to the two edges; but, since the edges are united, the seeds lie in a nearly straight line. However, when a legume splits open, some of the seeds remain attached to one edge and some to the other. The fruit of the peanut forms an exception in that it does not open at maturity. It is, however, a legume and not a nut.

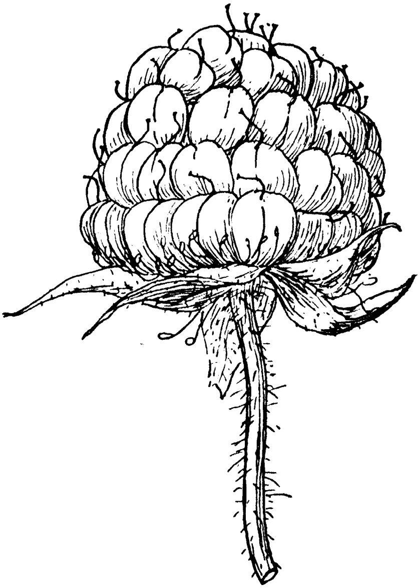


FIG. 362. Aggregate fruit of raspberry.

A *follicle* is like a legume except that it splits longitudinally along but one edge, whereas a legume splits along two opposite edges. The fruits of milkweed and columbine are follicles.

A *capsule* also is a dry fruit which cracks or breaks open at maturity; differently from a legume or follicle, it is developed from an ovary composed of more than one carpel. Capsules open in various ways when the seeds are mature; most commonly they split lengthwise into a definite number of segments, the number corresponding to the number of carpels. In the lily the split is along the line corresponding to the midrib of each carpel; in some other members of the lily family, the split occurs along each line of juncture between adjacent carpels. In a poppy capsule, the opening is by means of a circle of pores in the upper edge.

The fruit characteristic of the mustard family is the *silique.* It consists of two many-seeded carpels which separate at maturity, leaving between them a thin partition.

347. Aggregate Fruits. In contrast with a simple fruit is an *aggregate* fruit—a structure consisting of several or many closely

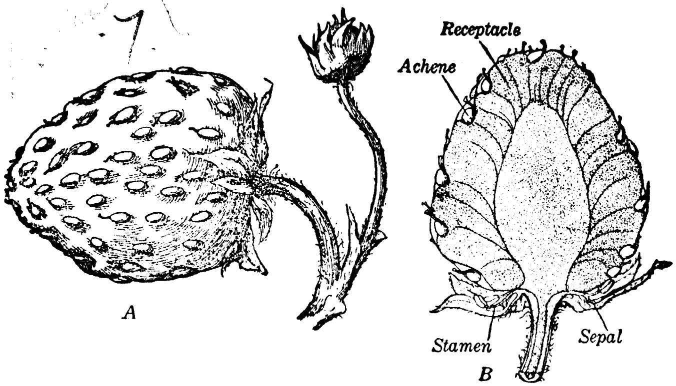


FIG. 363. Aggregate false fruit of strawberry, bearing many true fruits (achenes) on its surface. *A*, surface view. *B*, lengthwise section.

adherent fruits all developed from a single flower. Aggregate fruits include both true and false fruits. A raspberry (Fig. 362) is an aggregate of true fruits. The flower contains many pistils borne on the conical terminal portion of the receptacle. The ovary of each pistil develops into a small stone fruit. However, the many stone fruits are densely crowded and become so firmly attached during maturation that they adhere in a single mass when separated from the receptacle. A blackberry is also an aggregate fruit of this type, but the receptacle becomes softened and juicy and breaks off with the "berry."

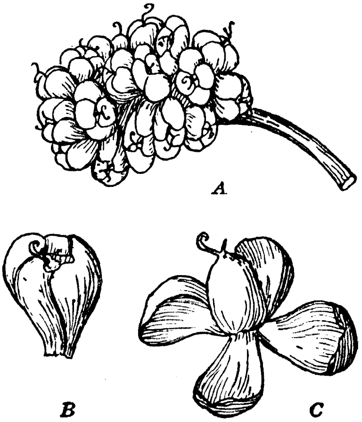


FIG. 364. *A*, multiple false fruit of mulberry. *B*, surface view of an individual false fruit. *C*, the same, with the fleshy sepals bent back, exposing the true fruit.

A strawberry (Fig. 363) is an aggregate false fruit developed from a single flower. The flower, like that of the raspberry, has a conical receptacle bearing many pistils. During maturation, the receptacle becomes greatly enlarged both beneath and between the pistils, the pistils so being

commercial varieties of pineapple do not contain seeds. At the apex of the whole multiple fruit are many greenish bracts in whose axils no flowers were borne.

The fig (Fig. 366) resembles a multiple fruit in including many individual fruits, each developed from a single flower. It differs in the fact that the individual fruits are not adherent. The many flowers of a fig are borne within the enlarged hollow, flask-shaped end of a branch. At the apex of the flask-shaped cavity is a small opening surrounded by several bracts. Some flowers are staminate, some pistillate, the distribution of the two kinds varying as between different varieties and species of fig. Each pistillate flower may produce a true fruit which is an achene similar to a true fruit of the strawberry but usually smaller and more nearly spherical. The end of the branch bearing the flowers becomes enlarged and is the fleshy part of the "fruit."

349. Classification of Fruits.

1. Simple:
   - (*a*) Fleshy:
     - Berry (grape).
     - Drupe or stone fruit (plum).
     - Pome (apple).
   - (*b*) Dry:
     - Indehiscent:
       - Achene (sunflower).
       - Grain (corn).
       - Nut (acorn).
       - Samara (maple).
       - Schizocarp (geranium).
     - Dehiscent:
       - Legume (pea).
       - Follicle (milkweed).
       - Capsule (poppy).
       - Silique (mustard).
2. Aggregate (raspberry).
3. Multiple (pineapple).

350. Dispersal of Seeds and Fruits. In a seed plant the seed represents the point in the life cycle at which a wider distribution of the species may chiefly be brought about. It follows that means for the dispersal of seeds to a greater or less distance from the plant

portions of its fruit, which are spongy and especially resistant to salt water. In consequence, the fruit may float for a long time without injury and may be carried by ocean currents to great distances.

Animals, too, play an important part in the dispersal of seeds and fruits. The fruits of many common weeds bear hooks or barbs (Fig. 368) by means of which they become attached to the

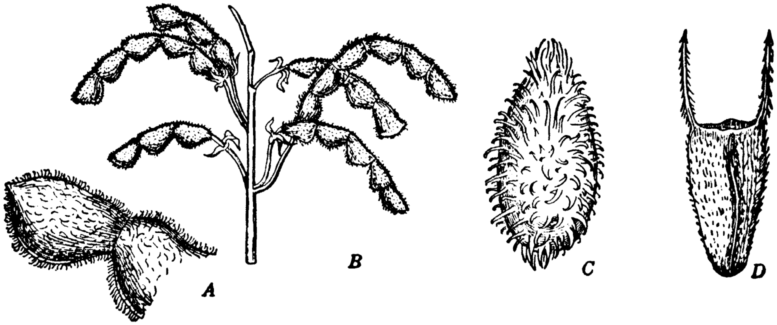


Fig. 368. Fruits which become attached to coats of passing animals. *A*, *B*, stick-tight (Hedysarum). *C*, cocklebur. *D*, beggar-tick. After Kerner.

coats of passing animals or to the clothing of human beings, being then carried to varying distances. Such outgrowths, in the cases of stick-tights, beggar-ticks, cocklebur, and stickseeds, are developments from the fruit coat; those of the burdock are the developed bracts of the floral head. The mud collected by the feet and legs of wading birds often contain seeds, which are thus distributed. Some fruits and seeds have sticky coverings by means of which they may adhere to the bodies of animals.

A very common means of dispersal is the production of edible seeds or fruits. Fruits of such trees as the walnut, hickory, and oak are carried away and hidden by squirrels, often in places where, if not eaten, the seeds may germinate. Other animals, especially birds, eat such edible fruits as berries. In such a case the seeds are usually swallowed; but these seeds are commonly protected by their coats from the action of the animal's digestive juices, and hence pass uninjured through its alimentary tract and are deposited at a distance from the plant that produced them.

Man has played a larger part in the distribution of seeds and fruits than have any of the lower animals. His part has consisted both in the intentional extension of the range of numerous cul-

tivated plants and in the accidental dispersal of seeds. Weed seeds are carried with the seeds of cultivated plants as well as in packing materials, in dust, and in other accidental ways, and are distributed by means of shipping lines and railways. Many weeds, like the Russian thistle and the Canada thistle, appear along railways, where their seeds have dropped from passing trains and thence spread to surrounding regions. Many troublesome weeds represent species that are not objectionable in their native lands but that, when carried to other countries, find favorable conditions for rapid multiplication.

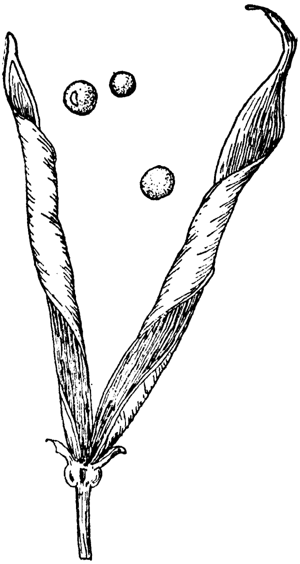


FIG. 369. Legume of a vetch, which opens suddenly and hurls the seeds.

Many plants have means by which their seeds, when mature, are explosively discharged from the fruits. The seeds of a violet are squeezed out by a contraction of the sectors into which the fruit coat splits. The fruits of vetches (Fig. 369) and of the witch hazel open suddenly so as to shoot out the seeds by a method comparable to that found in the violet. In the cranesbill, the fruit coat splits suddenly and its parts curl in such a way that the seeds are discharged. In touch-me-nots, the explosion of the fruit is brought about by the pressure of turgid tissues; and the seeds of the "squirting cucumber," with a juicy pulp in which they are imbedded, are ejected through an opening produced in the base of the mature fruit by its separation from the flower stalk.

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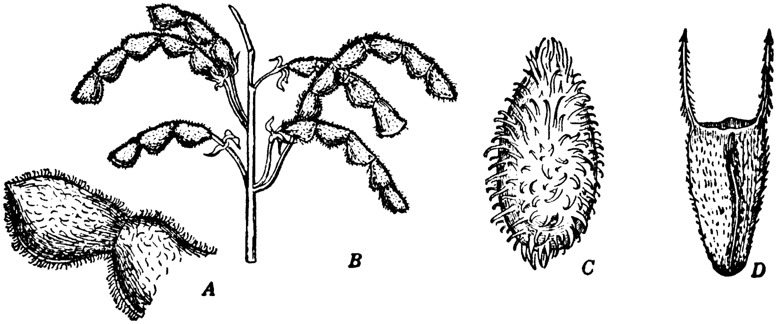

FIG. 368. Fruits which become attached to coats of passing animals. *A*, *B*, stick-tight (Hedysarum). *C*, cocklebur. *D*, beggar-tick. After Kerner.

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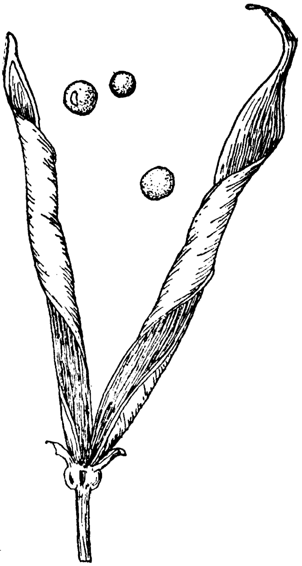

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CHAPTER XXXI

FLORAL TYPES AND THE FAMILIES OF ANGIOSPERMS

351. Arrangement of Flowers. The flowers of some plants are borne singly, as in the trillium and the may apple, at the end either of the stem or of a branch. In the latter case the branch, like most branches, commonly arises in the axil of a leaf. The stalk of the flower is a *peduncle*. Sometimes, as in Fuchsia, peduncles arise at various points along the stem, in the axils of foliage leaves. Often the leaves in whose axils peduncles and flowers are borne are small and sessile. Such leaves are known as *bracts*.

More commonly, however, flowers are borne in a cluster. In such a case, the stalk of the cluster is a peduncle, and the individual stalk of each flower is a *pedicel*. Pedicels, like peduncles, may arise in the axils of bracts. Two main types of flower cluster are recognized, depending upon the relative times at which different flowers of the cluster mature.

If the flowers which open first are those attached nearest the base of the peduncle, the cluster is *indeterminate*. It is so called because the floral axis can continue indefinitely to grow and to produce new flowers.

The form of an indeterminate cluster depends largely upon the relative lengths of pedicels and peduncle. If, as in the lily of the valley, the currant, and the choke cherry, both peduncle and pedicels are fairly long and all pedicels are of about the same length, the cluster is a *raceme* (Fig. 370, *A*). If the flowers are arranged as in a raceme, but the pedicels of the lower flowers are longer than those of the upper ones, so that the flowers are borne at nearly or quite the same level and the cluster is approximately flat-topped, it is a *corymb* (Fig. 370, *B*). In an *umbel* (Fig. 370, *C*) the pedicels arise at approximately the same level on the peduncle. Since the pedicels are all of the same or nearly the same length, an umbel, like a corymb, is flat-topped. If the peduncle is elongated, the intervals between the pedicels are short, and the pedicels themselves are short, the flowers therefore being borne close to the peduncle and to each other, the flower cluster is a *spike* (Fig. 370, *D*).

The common mullein and the dooryard plantain bear spikes. A *catkin* (Fig. 370, *E*), such as is borne by a willow or a poplar, is a spike with scaly bracts. If the peduncle is so shortened and thickened, as in the red clover or sunflower, that the cluster is more or less round- or flat-topped, it is a *head* (Fig. 370, *F*).

In a *determinate* flower cluster the central or terminal flower is the first to open, later flowers arising below the first one. The up-

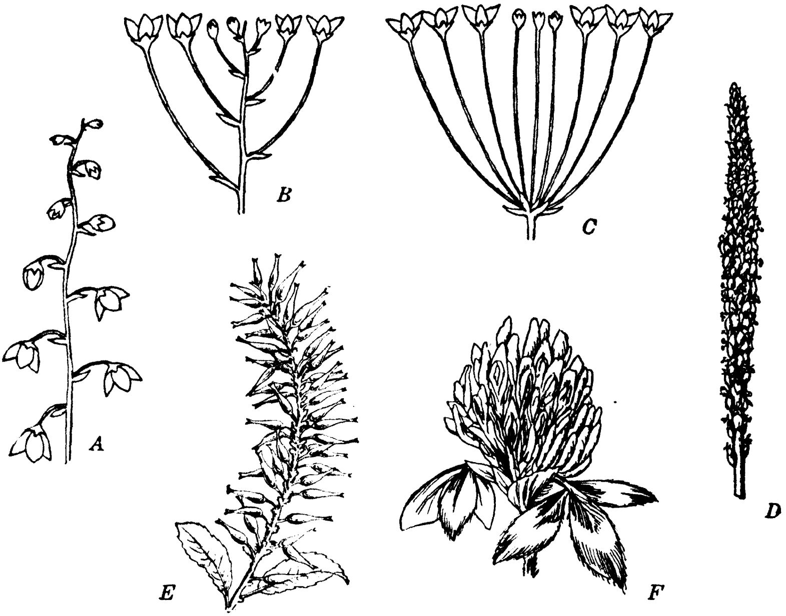


FIG. 370. Types of flower clusters. *A*, raceme (diagrammatic); *B*, corymb (diagrammatic); *C*, umbel (diagrammatic); *D*, spike of plantain, after Bailey; *E*, catkin of willow; *F*, head of clover, after Smalian.

ward growth of the main floral axis is terminated by the development of the central flower. A cluster of this type is called a *cyme* (Fig. 371, *A*). Cymes may resemble in form either racemes or corymbs.

Apart from the simple types of cluster already mentioned, there are many types of *compound* flower clusters. In these either the peduncles are branched, each branch bearing pedicels; or the pedicels are branched; or both peduncle and pedicels are branched. A common compound type is the *panicle* (Fig. 371, *C*) such as is borne by the oat and by many other grasses; other types

are compound corymbs, compound umbels, and compound cymes (Fig. 371, *B*).

352. Classification of Angiosperms. The division of angiosperms into dicotyledons and monocotyledons has already been mentioned. In arranging the members of these classes into orders, families, genera, and species, the structure and arrangement of the parts of flowers and fruits are chiefly used as bases of clas-

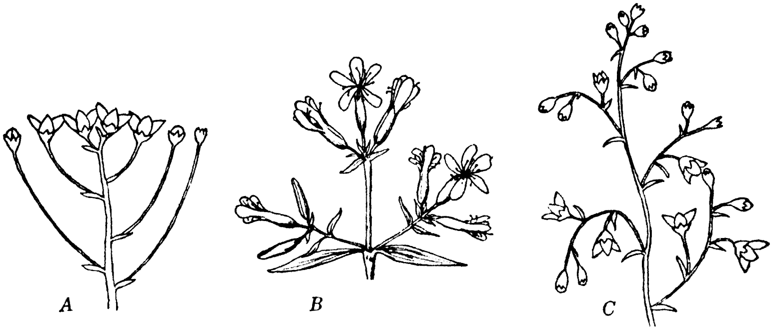


FIG. 371. Types of flower clusters. *A*, cyme (diagrammatic); *B*, compound cyme of Saponaria, after Rusby; *C*, panicle (diagrammatic).

sification. Monocotyledons include 45 families, divided into 1,500 genera and about 25,000 species. Dicotyledons include 240 families, 7,300 genera, and over 100,000 species. On account of the large number of angiosperms, only a few representative families can be described on the following pages. These families are selected either because of their large numbers of species or because they include especially well-known plants.

DICOTYLEDONS

353. Willow Family. A number of common trees and shrubs belong to a group of small families which are considered to be among the more primitive dicotyledons. One of these is the willow family, to which belong the willows (Fig. 372) and poplars. In all members of this family, flowers are borne in catkins of two kinds: one kind composed of pistillate flowers, the other of staminate flowers. Pistillate and staminate catkins are borne on separate plants. The flowers are very simple; a pistillate flower of the willow consists of one pistil borne in the axil of a hairy, scale-like bract. The pistil is composed of two united carpels, and the ovary contains a large number of ovules. A staminate flower,

borne likewise in the axil of a hairy bract, consists of two or more stamens, the number varying with the species.

The flowers of poplars are similar in general structure to those of willows. The fruit is a capsule which opens when the seeds are mature by a separation of its two constituent carpels. Each of the many seeds bears a circle of hairs at its base, forming a parachute-like structure that facilitates the carrying of the seed by winds.

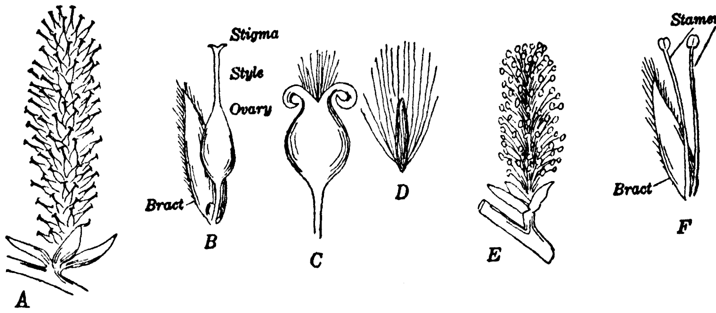


FIG. 372. Flowers, fruit, and seed of willow. *A*, pistillate catkin. *B*, pistillate flower. *C*, fruit. *D*, seed. *E*, staminate catkin. *F*, staminate flower.

Cottonwoods are species of poplar in which the hairs borne by the seeds are especially long and silky.

Among the relatives of the willow family are the walnut family, which includes the hickory, pecan, and walnuts; the birch family, to which belong hazels, alders, and birches; and the beech family, including chestnuts, beeches, and oaks.

354. Nettle Family. Among the many members of this family are a number of trees as well as herbaceous plants. The flowers are still simple but somewhat more complicated, especially by the presence of a calyx, than those of the willows. In most species the flowers containing stamens and those containing pistils are separate, the two kinds of flowers being borne either on the same or on different plants. The stamens are most commonly equal in number to the sepals; there is a one- (rarely two-) chambered ovary which forms a one-seeded fruit. The fruit is a samara, an achene, or a drupe.

The great majority of this family are tropical. The leaves of some members, including the nettles from which the family is named, have hairs that secrete an irritating acid. Among the trees of the family are elms (Fig. 373), hackberries, and mulberries.

The leaves of the white mulberry, which has been cultivated in Mediterranean countries since the twelfth century and in its native country, China, much longer, are used as food for silkworms. The fruits of this and of other mulberries are edible. Closely related to the mulberries is the Osage orange. Other members of the family are the hop and hemp. From hemp are obtained the drugs known as *hashish* and *cannabis*. Hemp is cultivated largely also for its bast fibers which are used in making ropes and fabrics. The family includes some other fiber plants. The bread-fruit tree of the tropics is a member.

FIG. 373. Elm twig bearing flowers and fruits. The flowers of the elm, differently from those of most members of the nettle family, are often "perfect"—that is, the same flower contains both a pistil and stamens.

Plants of this family frequently contain a milky juice (*latex*). The latex of the South American cow tree furnishes a nutritive beverage. The latex of several tropical members of the family is a source of rubber. The "India-rubber tree," the best-known rubber-yielding plant native to the eastern hemisphere, is a species of *Ficus*. Small specimens of this tree are grown as house plants in colder climates under the name of "rubber plant." (The tree most largely cultivated in plantations for rubber in various parts of the world is a member of the spurge family.) To the genus *Ficus* belong also the cultivated figs and the banyan tree (Fig. 31).

355. Pink Family. The families thus far mentioned are characterized for the most part by inconspicuous flowers, borne usually in close clusters, which either are naked (that is, without sepals or petals) or have sepals only. Many members of the pink family

have large, showy flowers borne singly or in small clusters and provided with both sepals and petals. They are mostly herbs, whereas the more primitive families include a large proportion of trees. The flowers in this family have usually five (sometimes four) sepals, as many petals if petals are present, and not more than twice as many stamens as sepals. The family includes some plants commonly cultivated for their flowers, the best known of which are the carnations and the related pinks and sweet williams (Fig. 374). The carnations are descendants of a European species that has long been cultivated. Among common wild plants of the family are the chickweeds, catchflies, campions, bouncing bet, and corn cockle.

FIG. 374. Flower cluster of sweet william, a member of the pink family.

FIG. 375. A buttercup.

356. Crowfoot Family. This, like the pink family, includes many species with showy, often solitary flowers having either a conspicuous calyx or a green calyx and a showy corolla.

The flower of a buttercup (Fig. 375) is fairly illustrative of the characteristics of this family. The receptacle is dome-shaped. The parts of the flower—sepals, petals, stamens, and pistils—are arranged spirally upon this receptacle, the sepals being lowest and

each succeeding set of parts arising from the receptacle above the set just outside it. The sepals are typically five, although there are variations from this number. Next within are five, or occasionally more, almost circular yellow petals, each bearing on its inner side at its base a small scale. Within the petals are an indefinite, rather large number of stamens, and within these a likewise indefinite number of pistils. Each pistil consists of a single carpel, and its ovary contains one ovule. A flower, therefore, produces a considerable number of achenes.

The flowers of most other members of the crowfoot family are similar in general plan to that of the buttercup. The numbers of the floral parts vary considerably. In a few species, including the larkspur, the flowers are irregular and bilaterally symmetrical, in consequence of the fact that the sepals of any flower are not all of the same shape, the same being true of the petals. Among the many familiar wild plants belonging to this family, in addition to various species of buttercup, are the anemones, hepaticas, marsh marigold, baneberry, clematis, meadow rues, and columbines. Some of the cultivated members of the family are the peony and species of columbine, clematis, and larkspur.

357. Mustard Family. The great majority of plants in this family are herbaceous; their roots, stems, or leaves in many cases contain sharp-tasting substances that make them valuable as condiments.

The flowers of the familiar shepherd's purse (Fig. 376) illustrate structures characteristic of the family. These flowers are borne in a long raceme. All the parts of each flower arise from a flattened receptacle. There are four green sepals; four small white petals, arranged in the form of a cross; and six stamens, of which two are shorter than the other four. The four long stamens seem really to represent two, each of which is branched close to its base. In the center of the flower is a single pistil composed of two united carpels. The ovary is divided by a partition into two chambers in each of which are many ovules. The fruit (silique) is flattened, approximately triangular in shape, and notched at the apex. Like the ovary from which it developed, the fruit is divided by a partition; at maturity the sides of the fruit separate from the partition, allowing the seeds to be scattered.

The flowers of members of the mustard family are all so similar to that of the shepherd's purse, being marked especially by the

cross-shaped corolla, that they are readily distinguished from those of other families. Members cultivated as sources of food are the turnip, rutabaga, radish, horse-radish, garden cress, and mustard. A very important species of the family is *Brassica oleracea* (Fig. 413), which by variation has given rise to the cabbage, cauliflower, kohlrabi, Welsh cabbage, and Brussels sprouts. Members grown for their showy flowers are the stocks or gilly-flowers, sweet alyssum, and candy-tuft. The water cress belongs in this family.

Fig. 376. A plant of shepherd's purse, and a raceme bearing flowers on its upper portion and fruits below.

358. Rose Family. This is one of the best-known families, because it includes a very large proportion of the common cultivated fruits as well as many plants with showy flowers. Among its members are herbs, shrubs, and trees.

The receptacle of the flower is either cup-shaped, bearing the carpels on its inner surface, as in roses and plums, or a cone-like protuberance as in the strawberry and raspberry. The sepals, petals, and stamens are borne on the outer portion of the receptacle. In one section of the family—that which includes the apple—the tube-like receptacle is united with the ovary, so that the outer parts of the flower—stamens, petals, and sepals—seem to be borne above the ovary.

The family is divided into seven sections, each characterized by its special type of flower and fruit. One section includes the spireas; another, the apple, hawthorn, and serviceberry; a third, the strawberry and cinquefoil; to a fourth belong raspberries and blackberries; to a fifth, the agrimony; the sixth section includes roses; and the seventh, the plum, cherry, peach, apricot, and almond.

The flower of the strawberry represents a comparatively simple type. The flower cluster is a few-flowered cyme. At the outside of each flower are five small green bracts which are not strictly parts of the flower. Next within is a whorl of five wedge-shaped green sepals; next, five rounded white petals; then three cycles of stamens (ten in the outer whorl and five in each of the inner two whorls);

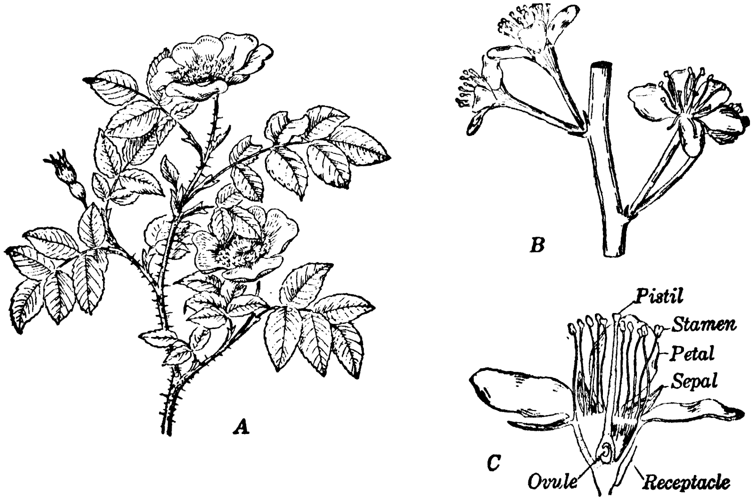


FIG. 377. Members of the rose family. *A*, a wild rose. *B*, flower cluster of plum. *C*, lengthwise section of a plum flower.

and finally, on the conically elongated central portion of the receptacle are many pistils, each consisting of one carpel, which are spirally arranged and closely packed together. Some cultivated varieties of strawberry have more than twenty stamens; other varieties have no functional stamens. The ovary of each pistil contains a single functional ovule; the style projects upward from the side of the ovary. After pollination and the union of gametes, the petals fall away and the stamens wither. Each ovary develops into an achene while the receptacle enlarges greatly both beneath and between the ovaries, forcing them apart. The enlarged receptacle becomes soft and pulpy, constituting the juicy portion of the edible "strawberry."

The flower of a wild rose (Fig. 377, *A*) is especially distinguished from that of the strawberry by the fact that the tube formed by the receptacle has the shape of an urn with a comparatively narrow

mouth. The tube becomes fleshy after gametic union, forming a rounded structure within which many dry fruits, each containing one seed, are enclosed. The flower has usually five petals and a large and indefinite number of stamens. Sometimes there are additional petals, making the number more than five; usually the additional petals replace stamens. By the selection of occasional plants with larger numbers of petals, and by a repetition of the selection when another similar variation occurred, cultivated varieties of roses have been developed with many petals and with few or no stamens.

A plum (Fig. 377, *B*, *C*) bears its flowers either singly or in small clusters. The tube formed by the receptacle only partly encloses the single pistil. There are five green sepals, five white petals, and numerous (usually 15 to 20) stamens. The ovary contains two ovules, only one of which develops into a seed. After the gametes have united, the outer parts of the flower fall away and the ovary develops into a drupe. The outer portion of the ovary wall forms the skin and the fleshy part of the fruit; the inner portion of the ovary wall forms the hard stone. The soft structure within the stone is the seed. The closely related cherry, apricot, and peach have flowers and fruits of the same type as the plum. The same is true of the almond, but the outer layer of its fruit, which corresponds to the skin and flesh of the plum, dries and is split off; the inner part of the fruit, corresponding to the stone of the plum, is the almond of commerce.

359. Pulse Family. This, comprising more than 12,000 species, is, with one exception, the largest family of seed plants. Its members, distributed throughout the world, include herbs, shrubs, and trees. A great majority of the species have bilaterally symmetrical (irregular) flowers of the type illustrated by the bean and pea, although some have regular or nearly regular flowers. All of them bear fruits of the kind known as a legume, developed from the ovary of a simple pistil.

The flowers of the sweet pea (Fig. 378) are borne in loose, open racemes. The peduncle arises from the axil of a leaf, and each pedicel from the axil of a minute bract. The five pointed sepals of a flower are united by their basal parts to form a cup, the three lower sepals being longer than the two upper ones. There are five white or colored petals, although there appear to be but four because two are intimately united. The upper petal (*standard*)

is broad and upright; the two lateral petals (*wings*) are borne one at either end of the standard; the two lower petals are united and their free margins are rolled inward to form a trough-like *keel.* The keel almost completely encloses the ten stamens; nine stamens are united by the expanded bases of their filaments into a sheath surrounding the ovary; the tenth (upper) stamen is separate. The pistil consists of one carpel whose structure suggests that of a leaf folded on its midrib so that its edges are brought together and united. The ovary contains several ovules, borne in two rows (apparently one) along the infolded and united edges of the carpel. The style curves upward nearly at right angles to the ovary. The stigmatic surface is along one face or edge of the style. This type of flower shows advances over the primitive condition in the union of sepals, the union of two petals, the union of the filaments of nine stamens, and in its bilateral symmetry.

FIG. 378. Sweet pea. The small bracts in whose axils the pedicels arose have disappeared.

After gametic union the petals and stamens fall off, and the ovary enlarges greatly as the seeds develop. When mature, the fruit formed by the growth of the ovary becomes dry and opens along two lines, one corresponding to the midrib of the carpel, the other to the line of junction of its two united edges.

As mentioned in Chapter XVIII, many members of the pulse family are characterized by a peculiar relation to certain bacteria which enables them indirectly to use the nitrogen of the air. In consequence of this relation, several of them are widely used forage plants, and their cultivation plays an important rôle in conserving and adding to the supply of nitrogenous food materials in the soil. Plants extensively grown for this purpose are the clovers, alfalfa, vetches, cowpea, and soybean. Another important characteristic of members of the family is the habit of storing reserve proteins in their seeds. It is because these contain a much

larger percentage of proteins than most other seeds—as well as large carbohydrate or fat reserves—that the seeds of the pea, bean, and lentil are important as human foods. A peculiar feature of the peanut is that after pollination its pedicels turn and grow downward, pushing the fruits into the soil where they ripen. Other well-known members of the family are the honey locust, black locust, wistaria, and mimosa. Among the woody tropical and subtropical species are many that supply lumber, resins, gums (including gum arabic), dyes (especially indigo), and drugs.

FIG. 379. Wild carrot; a compound umbel and (below) one of the simple umbels of which the compound umbel is composed.

360. Parsley Family. One general characteristic of this family is the arrangement of the flowers in umbels (Fig. 379). The individual flowers are small and usually white or yellow. Each has five sepals, five petals, and five stamens, all of which parts seem to be borne above the ovary. This appearance is really due to a union of the tube-like receptacle with the ovary. The single pistil is composed of two carpels united to form a two-chambered ovary, the two styles, however, being separate. The ovary develops into a hard, dry, two-parted fruit (schizocarp), each part containing one seed. When ripe, the two parts of the fruit separate. The family is characterized also by hollow internodes, by variously lobed or divided leaves with sheathing petioles, and by the secretion of volatile oils and resins which impart characteristic odors and flavors.

The leaves, fruits, and other organs of such species as parsley, celery, anise, dill, fennel, and coriander are used as foods or condiments because of their aromatic flavor. The carrot and parsnip are members of this family; so are several poisonous plants, including the water hemlock and poison hemlock,

some weeds such as the wild carrot, and several plants that supply drugs.

361. Mint Family. This family, with over 3,000 species, includes plants (mostly herbs) with usually four-sided stems and opposite leaves. In most species, each flower has five sepals which are united except at their tips; five petals united to form a more or less two-lipped corolla, the upper lip composed of two petals, the lower of three; four stamens, of which two are longer than the other two; and a pistil consisting of two two-lobed carpels surrounding a central style. At maturity four nutlets are formed, one from each carpel lobe.

FIG. 380. Spearmint.

The leaves of most species bear small glands containing a volatile oil which makes many of them useful as sources of flavors, perfumes, and drugs. Among cultivated members of the family are horehound, rosemary, lavender, sage, peppermint, and spearmint (Fig. 380). Coleus is cultivated because of its ornamental variegated leaves, and some species of Salvia are grown for their flowers. Horse mint and catnip are familiar weeds.

362. Nightshade Family. To the nightshade family belong many cultivated plants, of which the best known are the potato, tomato, and tobacco. The members are nearly all herbaceous with regular (radially symmetrical) flowers. A flower (Fig. 381) has five sepals united for a varying distance from their bases into a tube; five petals similarly united; five stamens which are united with the bases of the petals, and a pistil composed of two carpels. The fruit is a two-chambered capsule or berry, each chamber contain-

ing numerous seeds. The fruits of many species contain poisonous substances which are used in such drugs as belladonna, hyoscyamus, and stramonium, or narcotics such as characterize the tobacco. Even the tuber of the potato contains a small amount of a slightly poisonous substance. The large genus *Solanum* to which the potato belongs includes also the black nightshade, eggplant, horse nettle, and buffalo bur. The tomato, red peppers, ground cherry, and petunia are other members of the family.

FIG. 381. Apical portion of a plant of tomato, a member of the nightshade family.

363. Gourd Family. The plants of the gourd family are mostly herbs with thick, juicy stems that bear tendrils. The flowers (Fig. 382) are of two sorts: one with a pistil and rudimentary stamens, the other having stamens and a rudimentary pistil. Thus, in a family which stands relatively high in the evolutionary scale, the same characteristic of separate staminate and pistillate flowers appears that is found in the very primitive willow family. In some members of the gourd family both kinds of flowers are borne on the same plant; in other species, some plants bear usually only staminate, others usually only pistillate flowers. The flowers of both types are marked by a considerable degree of union of their parts. The sepals are united into a tube, and the petals are likewise united. The receptacle is completely united with the large ovary, which is thus distinctly below the levels of insertion of the other floral parts. The stamens also

FIG. 382. Portion of a plant of cucumber, a member of the gourd family, with flowers and a young fruit.

are often united by their anthers or by both anthers and filaments. The fruit is developed from the ovary together with the surrounding tissues of the receptacle, some of whose outer layers form a hard rind; many seeds are imbedded in the pulpy interior tissues. Most species are tropical or subtropical, and those cultivated in temperate regions have been introduced from warmer climates. Familiar members are the cucumber, pumpkin, squashes, watermelon, muskmelons, and gourds.

364. Composite Family. Not only is this family the most highly developed, it is also the largest family of angiosperms, containing some 23,000 species. Some composites, including the thistles, dandelion, and other very common weeds, have such efficient methods of distribution of their fruits, and produce fruits in so great numbers, that it is almost impossible to exterminate them. The name "composite" is given because the individual flowers are grouped closely together in a head which has the general appearance of a single flower, the more so because just below the head are green bracts that look like sepals. The tip of the peduncle is thickened and flattened into a broad, disk-like or cone-shaped flower-bearing surface.

The sunflower (Fig. 383) illustrates the floral organization typical of the family. At the edge of the flower-bearing disk are two or more cycles or very close spirals of overlapping green bracts. Just within these, and on the face of the disk, the flowers are borne closely packed together, each in the axil of a small bract. These latter bracts are arranged in incomplete open spirals. There are two types of flowers: the *ray flowers* are borne in a single or double row near the edge of the disk; the *disk flowers* cover the rest of the disk's surface. The receptacle of each disk flower is a hollow, wedge-shaped structure standing almost perpendicularly to the surface of the disk. It partly encloses, and is completely united with, the ovary. The pistil probably consists of two carpels, although the ovary contains but one functional ovule. Just within the sepals is a long, flaring tube having a conspicuous inflation about one fourth way up from its base. The portion of the tube below this inflation is formed by the united bases of the petals and stamens; the part above consists only of the united petals, which are separated at their tips into five blunt teeth. Above the level of their separation from the petals, the filaments of the stamens are separate from one another, but the anthers are united

by their edges into a long tube. The top of the ovary extends slightly above the top of the receptacle and completely fills the space at the center of the flower. The style, extending up through the corolla tube and the anther tube, terminates in two relatively large stigmas. A ray flower differs from a disk flower in having one side of its corolla greatly extended into a broad, flat structure. Frequently, also, in a ray flower the inflation near the base of the corolla tube is lacking; the stamens and style may be abortive, and there may be three sepals instead of two.

FIG. 383. The composite flower cluster (head) of a sunflower.

After the union of gametes, the style, stamens, petals, and calyx are shed, and the united receptacle and ovary enlarge greatly and become dry and somewhat hard. The single seed fills the space within, but is united to the ovary wall only over a very small area.

The composite type of flower cluster is the most specialized among the dicotyledons. The union, in effect, of the receptacle with the ovary, causing the outer parts of the flower to be borne above the ovary, is an advanced feature; the union of the petals into a corolla tube and that of the anthers into an anther tube also are advanced characters. The occurrence of flowers of two distinct types in the same head is likewise a highly specialized condition. In this latter respect, however, the sunflower is not typical of all composites. In the dandelion, as in a number of related genera, the head contains flowers of only one type which are similar in corolla form to the ray flowers of the sunflower.

Among the comparatively few members of the family that supply food for man are the lettuce, endive, chicory, salsify, artichoke, and Jerusalem artichoke. The sunflower is used as food

for livestock. Drugs are obtained from some composites, including camomile, calendula, arnica, tansy, and wormwood. Among ornamental plants of the family are the daisies, sunflower, dahlia, asters, and chrysanthemums. Some of the commonest wild plants and weeds, among them being conspicuous members of the autumnal flora, are asters, golden-rods, ragweeds, and thistles, the sagebrush, dandelion, beggar-ticks, yarrow, cocklebur, and burdock.

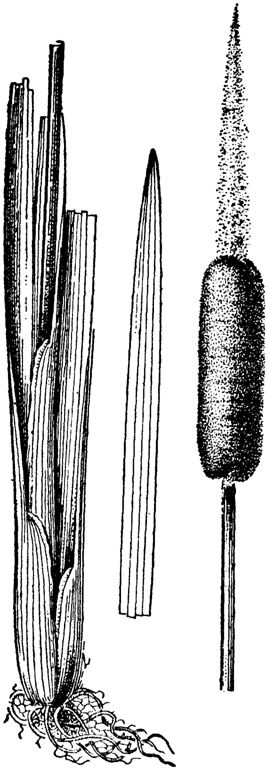


FIG. 384. Cat-tail. An aërial branch, a single leaf, and a flower cluster (spike).

Monocotyledons

365. Cat-tail Family. The monocotyledons seem to have arisen from some very primitive dicotyledon or dicotyledons. Within the class of monocotyledons, the course of evolution has substantially paralleled that which has marked the history of dicotyledons. In consequence, while preserving the characteristics that distinguish them from dicotyledons (§ 336), monocotyledons show very much the same steps in the evolution of floral structures that have been described for dicotyledons. The small cat-tail family is one of the most primitive among living monocotyledons, and may be thought of as holding much the same position in this class that the willow family occupies among dicotyledons.

The characteristics of the family are essentially those of the common cat-tail (Fig. 384), growing abundantly in wet, marshy places. This plant has a branching horizontal stem that lives in the mud from year to year, and each spring sends up aërial branches. Each such branch bears at its base long, sheathing leaves. At the upper end of an aërial branch is a long cylindrical spike of flowers. The central axis of a close cylindrical spike of this nature is a *spadix*. The flowers on the spadix are partly covered while young by long, thin, sheathing bracts (*spathes*); one spathe arises from the base of the spike, and

others may appear higher up, interrupting the cylindrical mass of flowers.

The flowers in the upper part of the spike are staminate, those in the lower part pistillate. Each staminate flower consists of two or three stamens borne on a short pedicel from whose lower part arise a number of hair-like outgrowths. A pistillate flower has a single pistil consisting of one carpel borne, like the stamens, upon a short, hairy pedicel. The ovary contains one ovule. After pollination, which is brought about by winds, the staminate flowers wither and disappear, leaving the upper part of the spadix bare. Each ovary may develop into an achene; the pedicel with its many hairs remains attached to the fruit when the latter is shed, and the hairs assist in the distribution of the fruit by winds.

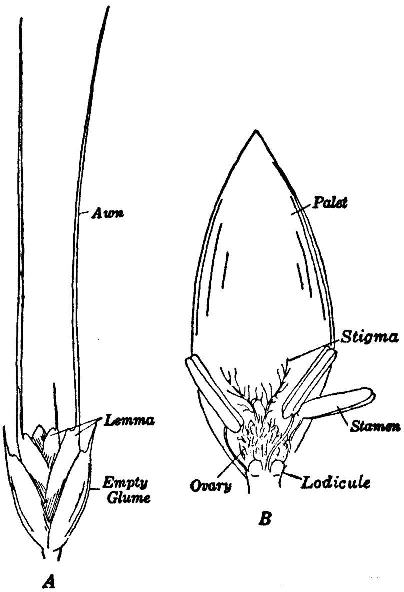


FIG. 385. Wheat. *A*, spikelet. *B*, single flower.

366. Grass Family. Here belong about 4,500 species which, like the cat-tails, have small, simple flowers and one-seeded fruits. In various respects, however, grasses show a considerably greater degree of specialization than do cat-tails, and they are very much more widely spread, different species being adapted to very different habitats. Like most monocotyledons they are herbaceous, although the tall, almost tree-like bamboos have more or less woody stems. The stems of grasses are jointed, the internodes being commonly hollow, and the leaves are alternately arranged in two vertical rows. Economically the most important grasses are the cereal grains, which include wheat, oats, barley, rye, corn, rice, and millet.

The flower of wheat (Fig. 385) may be taken as typical. The compound flower cluster, commonly called a head or spike, is made up of many small *spikelets*. Beginning at the base of a spikelet, and alternating on opposite sides of its central axis, are

two rather large bracts (*empty glumes*), and successively above these a few progressively smaller glumes (*lemmas*), each with a flower in its axis. A lemma has its concave face toward the axis of the spikelet, and the lower lemmas may bear long, stiff bristles (*awns*). Partly enclosed by each lemma is a thin bract (*palet*) which envelops the flower proper. The flower includes a pistil with a short ovary, and two short styles each terminating in a long, feathery stigma; three stamens with long anthers and thread-like filaments; and two small scales (*lodicules*) which may correspond to sepals. The ovary with its single ovule develops into a grain.

FIG. 386. A sedge.

In the corn and a few related grasses, stamens and pistils are borne in separate flowers; the staminate flower cluster of the corn is the tassel; the pistillate flower cluster is the ear.

In addition to cereals, the grasses of most practical interest are the sugar cane, sorghum, and broom corn; the bamboos, which in their native countries are used for a great variety of purposes; and many species which, like red top and timothy, are used for forage. The value of wild grasses for pasturage results in large part from their habit of growing together in great numbers, so that a considerable area may be covered by one or a few species. Their power of rapid multiplication by means of seeds as well as by the growth and branching of their underground stems makes some of the grasses, like so many of the composites, troublesome weeds. Some familiar weeds of this family are the wild oat, quack grass, and chess.

367. Sedge Family. Very similar to grasses in general appearance and in many characteristics are the sedges (Fig. 386). Most of them have three-sided solid stems, bearing leaves in three rows. The fruits are nut-like and one-seeded; the embryo, instead of being at one side of the seed as in a grass, is near the base and is entirely surrounded by endosperm. Some "rushes" and so-called "marsh grasses" belong to this family; so do the umbrella plant, and the papyrus which was used in ancient times in the manufacture of paper and from whose name the word *paper* is derived.

368. Palm Family. This is distinguished from other families of monocotyledons by the fact that most of its members have woody stems. Many of them are trees, each bearing at its tip a crown of large leaves. Some palms, such as the rattan palm, are climbing plants. Practically all palms are tropical or subtropical.

FIG. 387. Flower cluster and fruits of a fan palm (Washingtonia) of southern California.

In many species the flowers are borne on a spadix that is enclosed in a spathe. Some have branching flower clusters (Fig. 387). A single flower ordinarily has six perianth leaves in two whorls of three each, the outer whorl often being distinguished as a calyx, the inner as a corolla; there are usually six stamens in two whorls of three each, although in some species the stamens are fewer or more numerous than six; there are three carpels, forming either three separate pistils or one compound pistil. In many species staminate and pistillate flowers are separate and borne either on the same or on distinct plants. The fruit, usually one-seeded, is either a stone fruit as in the coconut, or a berry as in the date. The embryo is at one side of the seed; the seed contains also an abundant endosperm which is often hard. The hard part of the fruit of the date palm is the endosperm; the endosperm of another palm furnishes "vegetable ivory," used in the making of buttons.

The endosperm of the coconut, instead of being hard, constitutes most of the "meat" of the nut.

Coconut oil is made from copra, which is the dried meat of the coconut. Palm oil is derived from the fruits of certain species of western Africa and eastern South America. The betel nut, extensively chewed by natives of the East Indies, is the fruit of a palm. Sago is made by washing out the starch which is present in great quantities in the piths of some palms. Among the many other products of palms are fibers of various sorts, such as those from the petioles of the raffia palm; building materials, soap, wax (from the surfaces of stems), and various alcoholic drinks including arrack.

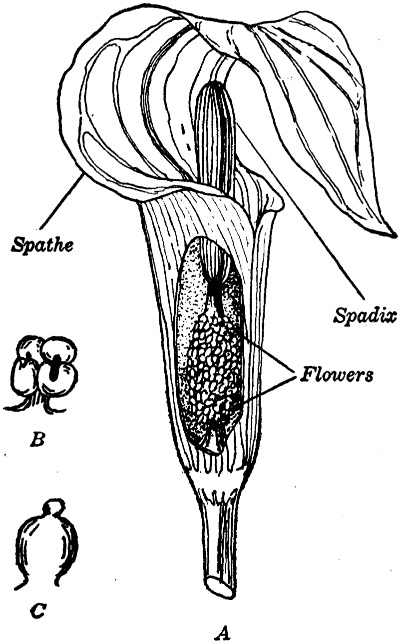


FIG. 388. *A*, flower cluster of jack-in-the-pulpit. *B*, staminate flower. *C*, pistil (constituting a pistillate flower).

369. Arum Family. Members of this family are characterized by having their flowers crowded on a spadix which is subtended or enveloped by a relatively large, persistent spathe; the spathe is often white or conspicuously colored.

A familiar native member of the family is the jack-in-the-pulpit or Indian turnip (Fig. 388). The flowers of this plant are of two sorts, the staminate flowers being borne on the upper part of the spadix, the pistillate flowers on the lower part. Not infrequently the flowers of one type abort, so that the functional flowers borne by a particular plant are all staminate or all pistillate. Each staminate flower consists of a varied number of short stamens; a pistillate flower is but a single simple pistil whose one-chambered ovary contains five or six ovules. The fruit is a scarlet berry with one or two seeds. The aërial shoot which terminates in the spathe and spadix, and which usually bears also two three-parted leaves, is

a branch growing from an underground stem. This stem is thick and approximately spherical; like various vegetative parts of many other members of the family, it has an intensely acrid taste.

Among familiar plants of the family are the skunk cabbage, sweet flag, and water arum. The arum family is most largely represented in the tropics, and many of the tropical species with showy or oddly shaped spathes are grown in greenhouses and as house plants. Among these are the calla lily, caladium, dracontium, and anthurium.

370. Lily Family. The flower of the hyacinth (Fig. 389) is fairly representative of the flowers of this family. The hyacinth has a raceme with a thick peduncle, each of the spirally arranged flowers being borne in the axil of a small bract. The perianth consists of two whorls of three leaves each, alike in color and shape and united at their bases to form a tube. The outer whorl of perianth leaves may be considered a calyx, the inner whorl a corolla. Near its middle the perianth tube is considerably constricted. Below the constriction the bases of the filaments of the six stamens are united with the perianth tube, but above the constriction each stamen is separate and distinct. Within the perianth tube but entirely separate from it is the pistil. This consists of three carpels and has a three-chambered ovary, a single style, and a three-lobed stigma. Along each line of junction of adjacent carpels their edges are much swollen, and each swollen edge bears a vertical row of ovules. Hence there are six rows of ovules extending through most of the length

FIG. 389. Aërial portion of a hyacinth plant.

of the ovary, and the ovules, together with the edges of the carpels on which they are borne, nearly fill the cavities of the ovary. The hyacinth flower represents a considerably advanced type in the partial union of the staminal filaments with the perianth tube, and in the complete union of carpels. After gametic union, the perianth and stamens are shed; the ovary enlarges greatly and becomes dry, splitting into three compartments each of which contains many seeds. Thus the fruit of the hyacinth is a capsule.

The flowers of other members of the family are in general similar to that of the hyacinth; the fruits of some are capsules, of others berries. Of the true lilies (members of the genus *Lilium*), some, such as the Easter lily, tiger lily, and Turk's-cap lily, have long been cultivated for their flowers. The same is true of many other plants of the family, including the lily of the valley, tulip, orange day lily, and yellow day lily. The greenhouse "smilax" and other species of asparagus are grown for ornamental purposes. Familiar wild plants are the trilliums, Solomon's seal, false Solomon's seal, dogtooth violet, and bellwort. Plants cultivated for food purposes are the asparagus and various members of the genus *Allium*, including onions, garlic, chives, and leeks. A few members of the family, including a species of Yucca and the dragon tree (Dracaena), have a special method of secondary thickening, referred to in § 46. The family includes also several drug plants and some plants which yield fibers.

371. Orchid Family.—In number of species this family, with over 9,000 members, is the largest among monocotyledons; few of its species, however, are abundant and some are very rare. Orchids are characterized by their remarkable bilaterally symmetrical flowers which show the greatest degree of union of floral parts found among monocotyledons. They occupy, therefore, a position among monocotyledons somewhat similar to that of the composites among dicotyledons.

The great variety of floral forms in the family seems to represent so many adaptations to insect pollination—often to pollination by insects of a certain size and even perhaps of a particular species. The flower of a lady's-slipper (Fig. 390) well illustrates the possibilities of development of an insect-pollinated flower. It has three sepals of which the two lowermost are united, and three petals, one of which, much larger than the other two, has the form of a slipper-like sac open at the top. The opening is partly closed by a

flap. The edges of the opening in front of the flap are curved inward. At the bottom of the sac on the inside are juicy hairs that are eaten by insects which make their way into the sac. On the lower side of the flap is the stigma; at either side of the stigma is an anther, whose pollen remains together as a sticky mass. A third stamen has no anther. Insects, if not too large, can make their way into the sac in front of the flap, but because of the curved edges of the opening they can not readily escape at the same place. If, however, like some bees, they are sufficiently strong, they can push out through the opening at either side of the flap. In such a case the insect brushes against the anther on that side and carries away its pollen mass. The same insect, entering another flower, brushes against the stigma, where the pollen mass may lodge.

FIG. 390. Lady's-slipper, a member of the orchid family.

Many orchids are grown because of their rarity or for the beauty of their flowers. Not many are otherwise useful, although the fruit of the vanilla, a tropical American orchid, supplies a well-known flavoring extract, and the dried tubers of some old-world orchids are used, under the name of *salep*, both as a food and as a drug.

Many tropical orchids are epiphytes—living high up on the trunks of trees. A few, including the coral root, possess no chlorophyll; with the aid of fungi in their underground parts they lead a saprophytic life.

CHAPTER XXXII

INHERITANCE AND VARIATION

372. Inheritance. It is a fact of common observation that offspring in most respects are similar to their parents, as well as to more distant ancestors. The general rule of resemblance between parent and offspring holds for one-celled as well as for many-celled plants and animals. This rule is implied when it is commonly said that offspring have inherited from their parents such characters as height, color of flower, or a tendency to respond in certain ways to stimuli. It will appear later that the statement that *characters* such as these are *inherited* is not strictly accurate. It would be more nearly correct to say that characters possessed by parents have reappeared in their offspring.

373. Independence of Characters. To a considerable extent, distinct characters behave independently in inheritance. That is, an individual plant may show one character that was present in a parent such as tallness, but may not display another character of the same parent such as flower color. The behavior of characters as something like separate units was demonstrated by the classical experiments of Gregor Mendel (1822–1884). While Mendel was not the first to observe such behavior, he devised a most important method of investigation of the subject in his studies on the common garden pea, the results of which were published in 1866.

Mendel first tested varieties of pea to determine whether they were pure-bred—that is, whether they regularly produced offspring like themselves. From among the varieties which proved pure in this sense he selected some which differed one from another in one or more sharply marked characters. These varieties were then crossed; that is, pollen from flowers of one variety was transferred to the stigmas of another variety.

In one experiment a tall variety of pea (six to seven feet high) was crossed with a short variety (¾ to 1½ feet). All the offspring of the cross were tall plants (Fig. 391). These immediate offspring constituted the *first filial* (F_1) *generation.* Mendel spoke of the tall character displayed by all the plants of the F_1 generation as *dom-*

inant. The short character, possessed by one parent but not by any of the F_1 generation, was *recessive.*

When plants of the F_1 generation, all tall, were self-pollinated, three fourths of their offspring in the *second filial* (F_2) *generation* showed the dominant character of tallness, but one fourth displayed the recessive character of shortness. The recessive character, which seemed lost in the F_1 generation, had reappeared.

When plants of the F_2 generation were self-pollinated, the short

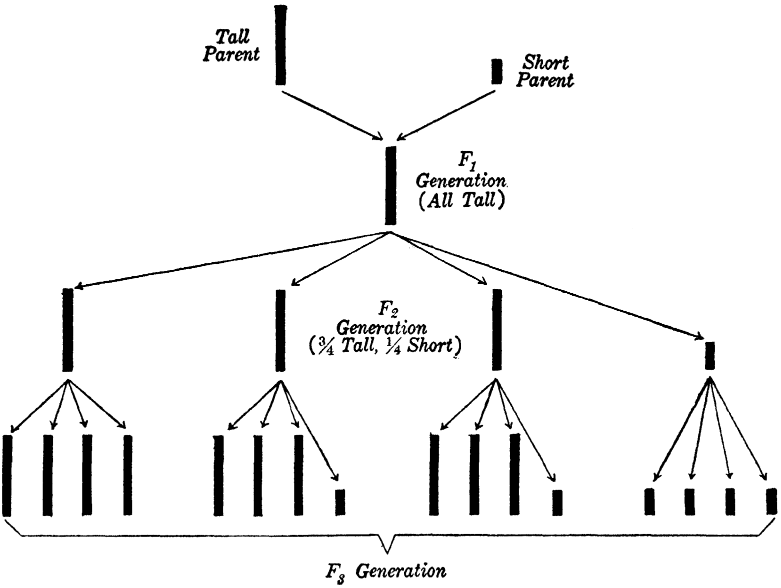


FIG. 391. Diagram illustrating the inheritance of tallness and shortness in Mendel's experiments with peas.

ones produced only short offspring (of the F_3 generation); one third of the tall F_2 plants produced only tall offspring; the remaining two thirds of the tall F_2 plants produced, like their parents of the F_1 generation, offspring of which three fourths were tall and one fourth were short.

In another series of experiments Mendel crossed a variety with purple flowers and one with white flowers. The purple-flower character proved dominant over the white-flower character. In the F_1, F_2, and F_3 generations this pair of characters behaved just as had tallness and shortness in the previous experiments. In all,

seven pairs of characters found in different varieties of pea were similarly tested.

Mendel studied also the simultaneous inheritance of two pairs of contrasting characters. When a tall variety with purple flowers and a short variety with white flowers were crossed, all the F_1 generation possessed both dominant characters—purple flowers and tallness (Fig. 392). The plants of the F_2 generation displayed all possible combinations of the two pairs of characters, and these

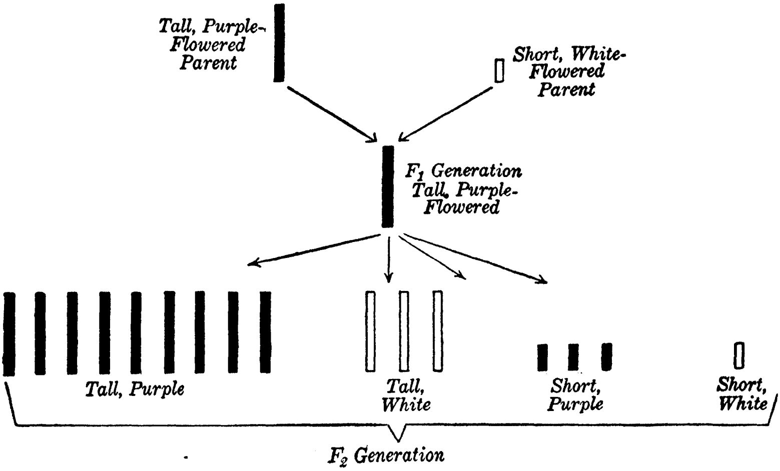


FIG. 392. Diagram illustrating the inheritance of tallness and shortness, purple and white flower color, in Mendel's experiments. Solid black rods represent purple-flowered plants; white rods, white-flowered plants.

combinations appeared in the proportions that would be expected if the characters of one pair (purple and white flowers) were transmitted independently of those of the other pair (tallness and shortness). The F_2 generation consisted, therefore, of plants of four classes in the proportions: nine tall with purple flowers; three tall with white flowers; three short with purple flowers; one short with white flowers.

Crosses between varieties differing in three pairs of characters—for example, purple and white flowers, plump and wrinkled seeds, yellow and green cotyledons—gave corresponding but of course more complicated results. The distribution of the characters of any pair among plants of the F_2 generation bore no relation to the way in which the characters of any other pair were distributed;

consequently there appeared in this generation different classes of individuals, in proportions that could be calculated in advance, possessing every possible combination of the characters of the grandparents.

Mendel's description of his experiments was almost completely overlooked until about 1900. Since its rediscovery, studies similar

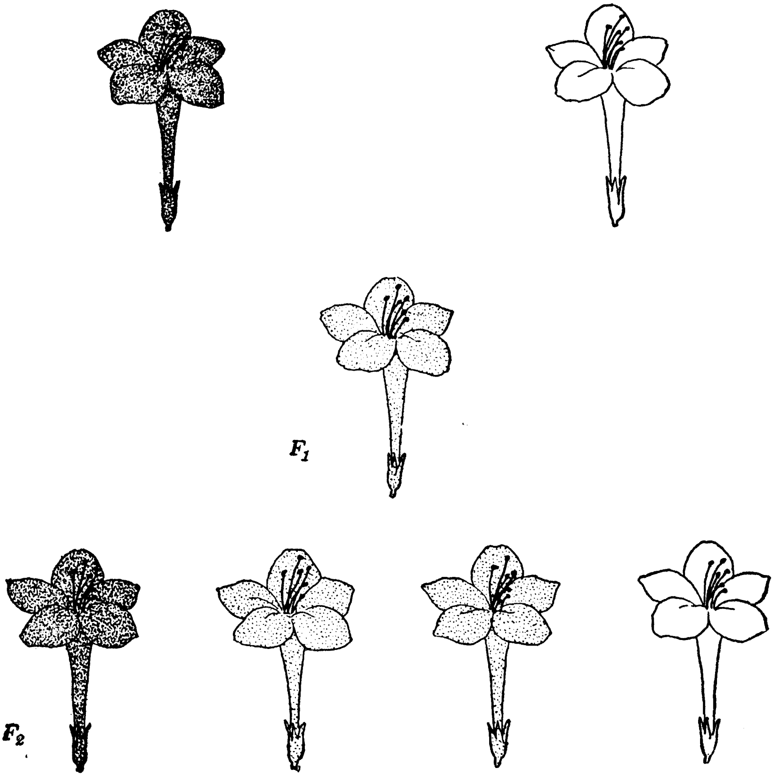


FIG. 393. Results of crossing a red- and a white-flowered four o'clock (Mirabilis). All the F_1 plants had pink flowers. In the F_2 generation ¼ had red, ½ pink, and ¼ white flowers.

to his have been made upon very many plants and animals. These studies have shown that in large measure characters behave in inheritance as though they were transmitted separately—being, as it were, reshuffled and arranged into varying combinations in each succeeding generation. Often, as in the peas studied by Mendel, a particular character of one parent is dominant in the F_1

generation over a contrasting character of the other parent. For example, red, blue, or yellow flower colors are in most cases dominant over white. Hairiness of stems is dominant over smoothness. Brown eye color in man is dominant over blue or gray.

In other instances, however, dominance does not appear; instead, the character that appears in the F_1 generation is in some degree intermediate between the characters of the parents. A case of this nature is that of a cross between a red and a white four o'clock (Fig. 393), which yielded offspring with *pink* flowers. When these F_1 pink-flowered plants were self-pollinated, their offspring in the F_2 generation were: one fourth red-flowered, one fourth white-flowered, and one half pink-flowered. The latter pink-flowered plants, like their parents, displayed the hybrid character. But whether the F_1 generation shows complete dominance of one parental character, partial dominance, or intermediacy, it is still true that both parental characters are in effect separately transmitted. In the case in question, the pink-flowered plants transmitted to some among their offspring the capacity to produce flowers like those of the original parents—namely, red and white.

374. Inheritance and Chromosomes. It was pointed out in Chapter XII that all inheritance must be by means of structures or substances that are transmitted from parent cell to daughter cell in the course of nuclear and cell division. It follows that offspring do not literally inherit *characters* from their parents—excepting, of course, the structural and functional characters of the spore or gametes which gave rise to the offspring. Apart from characters belonging to such cell or cells received from the parent or parents, all that the new generation inherits is certain *substances*, the presence of which in the cells of the offspring makes possible the development of characters like those of the parent. A pine tree does not literally inherit tallness; it inherits certain substances which give it the ability to grow tall.

It has appeared also that in the main the substances concerned in inheritance are carried in the chromosomes. There is evidence that substances or bodies (such as plastids) present in the cytoplasm play a part also in the transmission of hereditary possibilities. But the rôle of cytoplasmic structures in this respect seems so clearly to be subordinate to that of the chromosomes that the chromosomes are considered to constitute the essential *mechanism of inheritance.*

The fact is to be emphasized that chromosomal and cytoplasmic substances together do not finally determine the characters of a plant or animal. These substances endow the organism with certain possibilities of development; whether, or to what extent, those possibilities are to be realized depends upon the environment that surrounds the organism while it is developing. The actual characters that the mature plant or animal displays are therefore the result of an interplay of inherited tendencies and environmental influences. The pine tree above referred to can by appropriate treatment—such as keeping it in a pot too small to permit the free development of its root system—be induced to grow very slowly and to remain a dwarf throughout a long life; but the inherited capacity for tall growth remains and may be passed on to its descendants.

375. Characters and Genes. The fact that characters appear and reappear independently in large measure of one another has led to the assumption that characters are in some way represented by small portions or units of the hereditary substance. These units, called *genes*, are, if they exist, too small to be visible under any power of the microscope. Genes are thought of as borne in or upon the chromosomes—or, together, as perhaps constituting the whole chromosome substance. It is considered that the presence of particular genes in the chromosomes of a pea makes possible the development of tall or of short plants, of yellow or of green cotyledons, of purple or of white flowers.

Any pea plant, according to this conception, may possess in each of its nuclei two genes concerned with the appearance of tallness, having received one such gene from each parent; or two genes for shortness; or one gene for tallness derived from one parent and one for shortness coming from the other parent. If two genes for tallness are present, the plant is tall (external conditions being favorable); if two genes for shortness, the plant is short. If one gene for tallness and one for shortness are present, only the dominant gene expresses itself and the plant is tall. For the most part, other genes which affect various characters of the pea seem likewise to belong to contrasting pairs; as the genes for yellow and for green cotyledons, or those for purple and for white flowers. A similar statement can be made as to the genes that influence the characters of other species of plants and animals. In the pea more than 50 pairs of genes are recognized; in corn between 200 and

300, the largest number yet known for any species of plant. In a small fruit-fly (*Drosophila melanogaster*) the number is approximately 500—the largest known for any animal.

What has been said may seem to imply that each character is influenced by but one pair of genes, and that each pair of genes is concerned in the production of a single character. The facts, however, are by no means so simple. In general, any gene affects not one character alone, but several or many characters. For example, the gene in the pea which causes the production of a purple flower color also influences the color of the seed coat and that of the stem in the leaf axils. Conversely, each character is the result of the activity of several or many genes. Three pairs of genes are recognized which affect flower color in the pea; Mendel's work dealt with one of these pairs. Similarly, three pairs of genes, of which one pair was involved in Mendel's experiments, influence the color of cotyledons. Eye color in Drosophila is said to be affected by at least fifty genes. The total constitution of a plant or animal, then, depends upon the complicated interaction of many genes, whose effect in turn is conditioned by the environment.

Even though a character is influenced by several genes, it may be inherited as though it were represented by but one pair. This is explained by the fact that two races or varieties of a species may be alike with reference to all save one pair of the genes that noticeably affect the character in question. For example, if, as in Mendel's work, plants are crossed that differ with respect to only one pair of genes that may influence height, then tall and short plants will appear among the later generations in the same proportions as though only that one pair of genes affected height. For the purposes of the experiment these may be referred to as a gene for tallness and a gene for shortness.

376. Genes and Chromosomes. It has been seen (Chap. XXV) that each cell of a sporophyte contains 2 n chromosomes, of which n are of maternal and n of paternal origin. Each maternal chromosome *corresponds* to a particular paternal chromosome in the sense that the two bear the same or corresponding genes.

Suppose that two pure-bred plants, one tall and one short, differ, like those Mendel worked with, in one pair of genes. The chromosomes of one pair in each cell of the tall plant carry each a gene for tallness. Each chromosome of the corresponding pair in the cells of the short plant carries a gene for shortness. When the

reduction divisions occur in the tall plant, each macrospore and each microspore receives one chromosome bearing a gene for tallness. Since the spores give rise to corresponding gametophytes, each cell of a macrogametophyte (including the egg) and each cell of a microgametophyte (including the male gametes) contains in its single set of chromosomes one which carries a gene for tallness. Similarly, each spore, gametophyte, and egg or male gamete produced by the short plant has a chromosome bearing a gene for shortness.

Suppose now that the two plants are crossed. An egg from the tall plant, one of whose chromosomes carries a gene for tallness, unites with a male gamete from the short plant, one of whose chromosomes bears a gene for shortness. The zygote so formed has among its 2 n chromosomes one pair bearing respectively a gene for tallness and a gene for shortness (Fig. 394). A similar pair of chromosomes is present in each cell of the F_1 sporophyte that develops from this zygote. Since the gene for tallness is dominant, the sporophyte is tall.

When the reduction divisions occur in this sporophyte, the chromosomes of the pair in question (like those of other pairs) conjugate and separate. Hence half the macrospores, and the macrogametophytes and eggs to which they give rise, receive each a chromosome bearing a gene for tallness, and half receive each a chromosome carrying a gene for shortness. Similarly with the microspores, microgametophytes, and male gametes; half receive a gene for tallness, half a gene for shortness. If eggs of the two classes unite indiscriminately with male gametes of the two classes, the result will be (as shown in Fig. 394) that one fourth of the zygotes formed, and of the F_2 sporophytes developing from them, receive each two genes for tallness; these will be tall plants. One half of the F_2 sporophytes receive each one gene for tallness and one for shortness; these also will be tall plants. The remaining fourth of the F_2 sporophytes receive each two genes for shortness; they will be short plants.

A comparison of Figure 394 with Figure 391 shows how the behavior of the chromosomes and of the genes they carry explains Mendel's results in this and similar experiments.

If the parents of the cross differ in two genes instead of one (for example, in genes for tallness and shortness, for purple and white flowers), these genes being borne on chromosomes of dif-

ferent pairs, the story will be as shown in Figure 395. In this case the F_1 sporophytes will give rise to four kinds of macrospores, macrogametophytes, and eggs; and to four kinds of microspores,

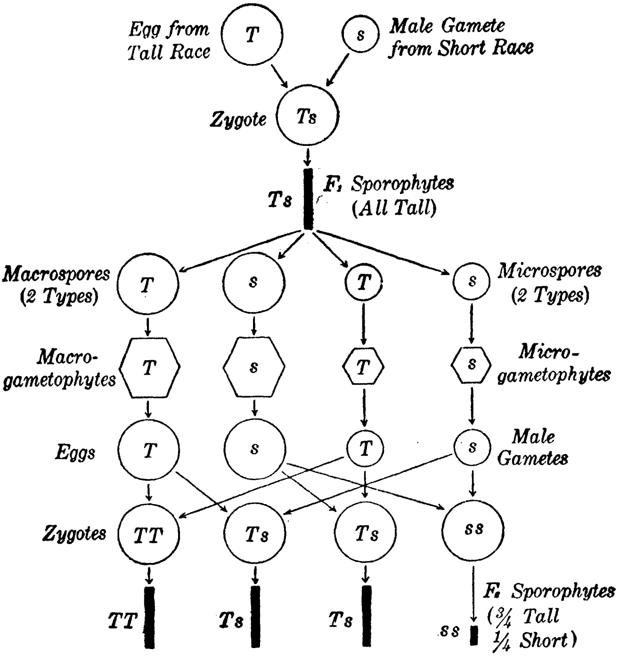


FIG. 394. Diagram illustrating the transmission of genes for tallness and shortness, borne on chromosomes of 1 pair. Each original parent contributed, through its gamete, 1 chromosome of the pair. The 2 chromosomes are separated in the reduction divisions, half the macrospores and half the microspores receiving the chromosome bearing a gene for tallness, the other half of the macrospores and microspores receiving the chromosome bearing a gene for shortness. These spores give rise to gametophytes, and these to gametes, containing corresponding chromosomes; hence there are 2 kinds of eggs and 2 kinds of male gametes. The result of haphazard unions between eggs and male gametes is the production of zygotes, and hence of sporophytes, of which ¼ have 2 genes each for tallness, ½ have each 1 gene for tallness and 1 gene for shortness, ¼ have each 2 genes for shortness. Sporophytes of the first 2 classes are tall, tallness being dominant; those of the third class are short.

microgametophytes, and male gametes. The indiscriminate union of eggs of four kinds with male gametes of four kinds will result in the formation of nine types of zygotes, and hence of nine types (although in appearance only four) of sporophytes, in the propor-

tions shown in Figure 396. The behavior of chromosomes and genes as illustrated in Figures 395 and 396 explains Mendel's results when he crossed plants differing in two characters (Fig. 392).

377. Linkage. In the case last referred to of a cross between parents differing in two pairs of characters, the different combina-

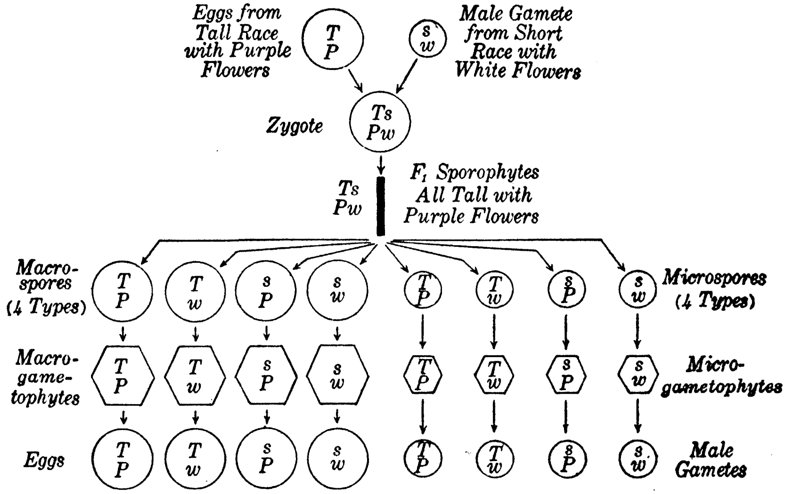


FIG. 395. Diagram illustrating the transmission of 2 pairs of genes, borne on different pairs of chromosomes. Each original parent contributed, through its gamete, 1 chromosome of each pair. Chromosomes of 1 pair bear respectively genes for tallness (T) and for shortness (s); those of the other pair, genes for purple (P) and for white (w). The F_1 sporophyte produces 4 types of macrospores and 4 types of microspores. These spores give rise to macrogametophytes of 4 types, producing each its own type of egg; and to microgametophytes of 4 types, producing each its own type of male gamete. The result of haphazard unions between different types of eggs and male gametes is shown in the following figure.

tions of genes occurring in the F_2 generation result from the fact that all the genes are borne on separate chromosomes. If, however, two genes (A and B) are carried on the same chromosome and genes a and b (respectively recessive to A and B) on the other chromosome of the same pair, a very different result would be expected. Since the chromosomes of this pair conjugate and separate in the reduction divisions in an F_1 plant, only two types of macrospores, and hence of eggs, would be produced. Half the eggs would possess each a chromosome bearing genes A and B, half would possess a chromosome bearing genes a and b. The micro-

spores, and hence the male gametes, would likewise consist of two classes: half having genes *A* and *B*, half having genes *a* and *b*. In other words, the spores and gametes would be expected to possess the same combinations of genes that were present in the original parents. The indiscriminate union of eggs and male gam-

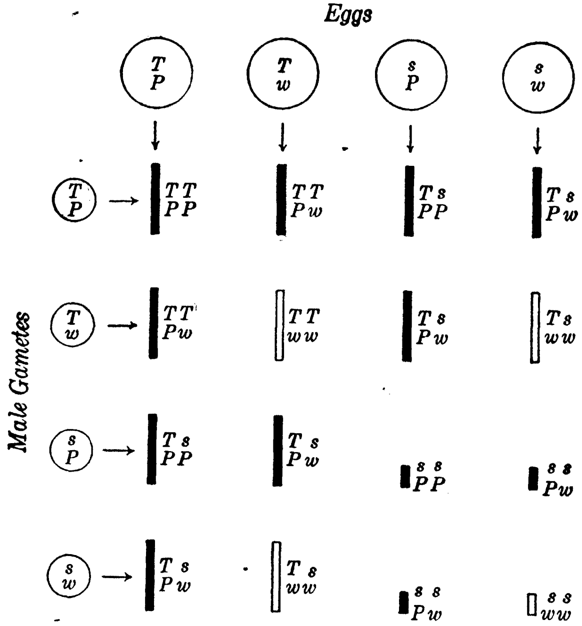


FIG. 396. Diagram showing the result in the F_2 generation of haphazard unions between eggs and male gametes produced by the F_1 generation of a cross between a tall, purple-flowered and a short, white-flowered plant (see preceding figure). Nine different combinations of genes occur in the F_2 zygotes and resultant sporophytes: *TTPP*, *TTPw*, *TsPP*, *TsPw*, *TTww*, *Tsww*, *ssPP*, *ssPw*, and *ssww*. Since *T* is dominant over *s*, and *P* over *w*, plants of the first 4 of these classes are tall and purple-flowered; those of the next 2 classes, tall and white-flowered; those of the next 2 classes, short and purple-flowered; and those of the last class, short and white-flowered. Hence *in appearance* there are 4 classes of F_2 sporophytes, in the proportion 9 : 3 : 3 : 1.

etes would then result in the production of but three types of zygotes (and F_2 sporophytes) instead of nine.

If the original parents differed in three, four, or more genes, all these genes *being borne on the same chromosome*, a similar result would be expected. The genes which distinguish each parent,

being carried on the same chromosome, would tend to remain together from generation to generation; they would be *linked*, or would constitute a *linkage group*.

If the original parents differed in many genes, some borne on the chromosomes of each pair, those carried on any particular chromosome would tend to pass together from generation to generation. There would be as many linkage groups as chromosome pairs. It has in fact been found that some of the genes of the pea tend to pass from generation to generation in groups. The question has not yet been tested for all the recognized genes; because to determine with what other genes a given gene is linked requires experiments carried on for some time and on a large scale. Thus far six linkage groups of genes are recognized in the pea of the seven groups expected. The corn has ten pairs of chromosomes; ten linkage groups are recognized. The species of Drosophila already mentioned has four pairs of chromosomes. Of approximately 500 pairs (or series) of genes known for this fly, the linkage relations of a large proportion have been determined. All are found to be referable to four linkage groups. In no species of plant or animal have the genes been found to constitute a number of linkage groups greater than the number of chromosome pairs.

378. Crossing Over. Each of the linkage groups just referred to consists of genes which *tend* to remain together. Although cases of real or apparent *complete linkage* are known, it is the general rule that any two linked genes now and then become separated. For example, a gene for plump seeds in the pea (dominant over wrinkled seeds) is linked with one for the presence of leaf tendrils (dominant over the absence of tendrils). If a plant with plump seeds and tendrils is crossed with one having wrinkled seeds and no tendrils, and if the genes concerned were completely linked, the plants in the F_2 generation would be of two classes: some with plump seeds and tendrils, some with wrinkled seeds and no tendrils. As a matter of fact, the F_2 generation produced in one such experiment consisted of 319 plants with plump seeds and tendrils, four with round seeds and no tendrils, three with wrinkled seeds and tendrils, 123 with wrinkled seeds and no tendrils. The occurrence of small numbers of plants of the second and third classes indicates that, in about one of every 64 spore mother cells in the F_1 plants, genes which were linked, and therefore were presumably borne on the same chromosome, became separated.

Such an occasional separation of two linked genes seems to take place in that early period in the first reduction division at which the chromosomes of each pair are closely associated. At this stage, as was pointed out in § 274, there is a possibility of some interchange between the chromosomes of each pair. Under very favorable conditions of fixation and staining, chromosome

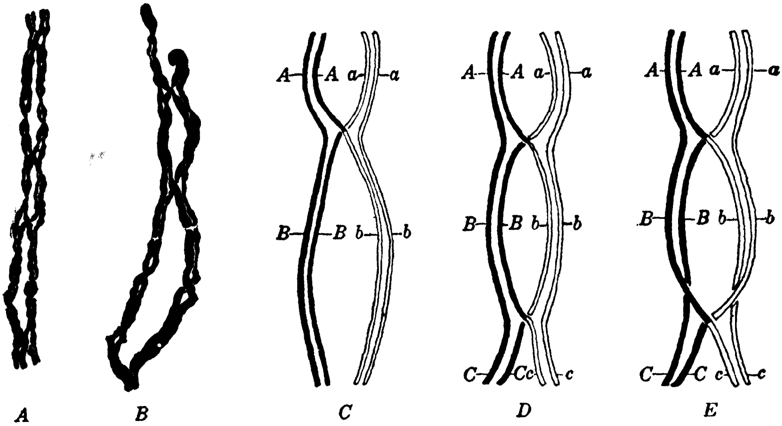


FIG. 397. Crossing over. *A* and *B*, chromosome pairs at an early stage of the first reduction division in a macrospore mother cell of lily. Interconnections between half-chromosomes. Drawn by D. C. Cooper. *C*, diagram illustrating a single crossing over. *D*, double crossing over. *E*, crossing over (above) between half-chromosomes, and (below) between the other halves of the same chromosomes.

arrangements like those shown in Figure 397, *A*, *B*, have been seen in a few plants and animals. This figure represents a stage approximately corresponding to that shown diagrammatically in Figure 283, *C*. Each chromosome of the pair is double, and at certain points one of the halves of each chromosome is interconnected with one half of the other chromosome of the pair. Appearances of this nature in pairing chromosomes, together with the facts of partial linkage, indicate that in the early stages of the first reduction division parts of two paired chromosomes may be exchanged.

Figure 397, *C*, shows diagrammatically how, in the simplest possible case, such *crossing over* would bring about new combinations of genes. The dominant genes *A* and *B* are borne on one chromosome and the recessive genes *a* and *b* on the other chromo-

some of the same pair. A crossing over occurs between one half of each respective chromosome at a point between *A* and *B* (and between *a* and *b*). When the separation of the four half-chromosomes is finally effected by the first and second reduction divisions, one of the four nuclei formed by these divisions will contain a chromosome bearing genes *A* and *B;* one nucleus, a chromosome bearing *A* and *b;* one nucleus, a chromosome bearing *a* and *B;* and one a chromosome bearing *a* and *b*. With respect to the genes on this pair of chromosomes, the macrospore or microspore nuclei formed would be of four different kinds.

Figure 397, *D* and *E*, show some of the more complicated cases of crossing over which have been found to occur.

In the study of linked genes in the pea and other organisms, various proportions of crossing over are found. It is considered that the proportion of crossing over occurring between any two linked genes is some measure of the distance between them on the chromosome—those genes showing the larger proportion of crossing over being farther apart than those between which crossing over is relatively rare.

The frequency with which crossing over occurs is affected by temperature, as well as by X-rays and radium emanations.

379. Variation. While resemblance between ancestors and offspring is general, it is not universal. Offspring, though like their parents in most respects, always differ, usually in minor ways, from the parents as well as from other members of the same family. The appearance of such differences is *variation.* The characters of an individual *vary* in some measure from the characters of the parent or parents.

In most cases a character in respect to which an individual differs from its parent is not transmitted to future generations; the change that has appeared is not permanent. Variation of this non-heritable type seems in general to result from the development of the new individual under an environment different from that which surrounded its ancestors. Since under natural conditions no two environments are exactly alike, it is not surprising that no two wheat plants, however similar in inheritance, are precise duplicates. The effect of environment in causing variations may, therefore, be observed in any field of wheat or corn or in any community of human beings; in each of these cases many differences between individuals result from differences in inheritance; but many result

from differences in environment (see, for an extreme example of variation due to environment, Fig. 398).

But sometimes a new character, once it has appeared, is passed on to later generations in the same way as are older characters. While variation producing such heritable changes is much less frequent than variation of the non-heritable sort, it occurs often enough to play an important part in giving rise to new kinds of plants and animals. Examples of heritable variation are the appearance of a tree bearing smooth peaches (nectarines), whose ancestors bore peaches of the downy type; the occurrence of a white-flowered plant whose ancestors were red- or blue-flowered; or of a beardless wheat plant in a regularly bearded variety. Such an individual may become the starting-point of a new race; if the new race differs sufficiently from the older race from which it arose, it may be considered a new variety or even a new species. Innumerable varieties of cultivated plants and of domestic animals have originated with individuals in which, in consequence of variation of this nature, a new heritable character or a new combination of such characters appeared. Doubtless many wild varieties and species have had a similar origin, although the fact can be known only when, as in cultivated plants and domestic animals, the first appearance of a new character or character-combination is actually observed.

FIG. 398. Influence of environment upon external form (producing non-heritable variation). *A*, dandelion plant grown at a low altitude. *B*, plant of the same species grown at a high altitude. Both to the same scale. Redrawn from Bonnier.

As has been seen, variation of the non-heritable type is largely

if not entirely due to the environment. It is not so clearly true that heritable variation is similarly caused; because the environment seems not, as a rule, to affect the hereditary substances in the chromosomes. It is true, as will appear hereafter, that under experimental conditions certain environmental factors may cause changes in the number and constitution of chromosomes and in

A *B*

FIG. 399. *Oenothera Lamarckiana* (*A*) with 14 chromosomes, and a variant form, *Oenothera gigas* (*B*) with 28 chromosomes. After De Vries.

the constitution of genes. But to what extent, if at all, such factors produce similar effects in nature is still unknown.

While the underlying causes of chromosomal and genic changes which result in heritable variation are yet obscure, much has been learned regarding the nature of these changes. A few types of change now fairly well known will be mentioned.

380. Changes in Number of Chromosome Sets. In 1895 there appeared in De Vries' cultures of an evening primrose (*Oenothera Lamarckiana*) a plant which differed from the parent in being larger in most of its parts, including stem, leaves, and flowers (Fig. 399). Whereas the parent species has 14 (2 n) chromosomes,

this giant plant possessed 28 (4 *n*). Giant forms with 4 *n* chromosomes have appeared suddenly in cultures of various plants, including two other species of evening primrose, the tomato, and tobacco. Many cases are known in nature of closely related species, one of which has twice as many chromosomes as the other. There is little doubt that in many of these instances a sudden doubling of the chromosome number occurred.

It has many times been observed that a nuclear division, either vegetative or reductional, was not concluded; instead, the chromosomes, which had begun to separate, were all brought together in a newly organized nucleus. The new nucleus then possessed a doubled complement of chromosomes. Such stoppage of nuclear division, with consequent doubling of the chromosome number, has been brought about experimentally in some organisms; notably in Spirogyra by cooling or anesthetizing the filaments, and in onion root tips by treatment with chloral hydrate and with other poisons or narcotics. A similar disturbance of division evidently occurs not infrequently in nature, although from unknown causes. In all probability many occurrences of giant forms, as of the evening primrose, are to be traced back to an uncompleted nuclear division; although this is not the only way in which the chromosome number may be doubled or otherwise increased.

Other observed occurrences, among the offspring of parents with 2 *n* chromosomes, have been the appearance of plants with 3 *n*, 5 *n*, 6 *n*, and other multiples of *n* chromosomes. It has happened too in a number of genera, likewise including evening primroses, the tomato, and tobacco, that a plant (sporophyte) appeared with only *n* chromosomes. Such a plant seems to have developed from an egg which had failed to unite with a male gamete and which had, therefore, but *n* chromosomes.

Any sporophyte with an even number of chromosome sets (as 2 *n* or 4 *n*) may conceivably produce offspring substantially like itself. This is because when the reduction divisions occur in such a plant all the chromosomes can arrange themselves in pairs of corresponding chromosomes; hence functional spores and ultimately functional gametes may be produced. If, however, a plant has an odd number of chromosome sets (as *n* or 3 *n*), regular pairing can not take place. The spores and gametes of such a plant, if spores and gametes are produced at all, will receive variable numbers and combinations of chromosomes. Most of the gametes,

sometimes all, will not function; if any do function, the resultant offspring are highly variable. It follows that a sporophyte with n or 3 n chromosomes can not give rise to a constant variety or

A *B* *C*

FIG. 400. Varieties of wheat representing 3 classes; below, a microspore mother cell from each variety. *A*, a wheat with 14 chromosomes (7 pairs). *B*, one with 28 chromosomes (14 pairs). *C*, one with 42 chromosomes (21 pairs). Figures of microspore mother cells from Sax.

species, unless the ordinary methods of reproduction are replaced by some form of multiplication (vegetative or other) which does not involve the union of gametes. Exactly this seems to have happened in some of the roses mentioned below.

In many genera, series of species are found whose chromosome numbers are multiples of a common basic number. One such genus

is that of the wheats. All known species and varieties of wheat fall into three classes (Fig. 400). Those of one class have 14 chromosomes; those of another class 28; those of a third, 42. Those with 28 and those with 42 chromosomes seem to be descended from plants with like numbers that arose as variants from races with 14; although there are suggestions that hybridization with plants of a related genus having likewise 14 chromosomes may have been concerned in the production of the species with higher numbers. The roses provide a similar but more extensive series. Some species and varieties have 14 chromosomes; others have respectively 21, 28, 35, 42, and 56.

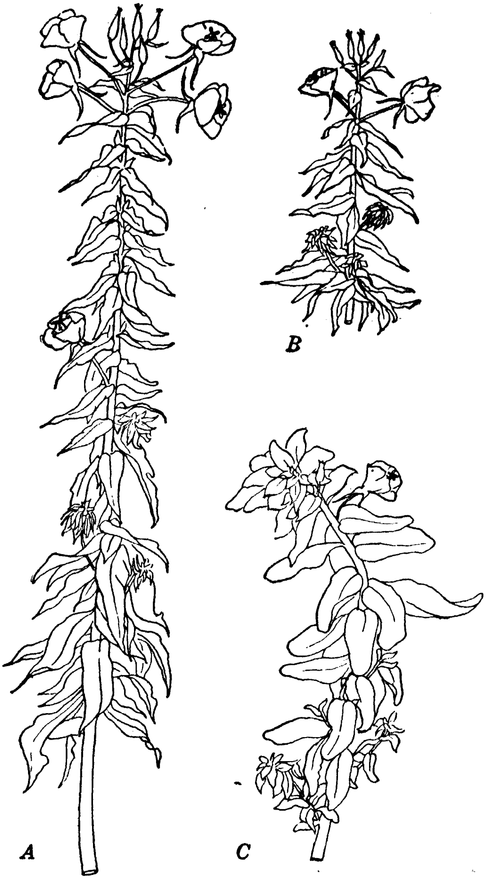


FIG. 401. Shoots of *Oenothera Lamarckiana* (*A*) and of 2 variant forms derived from it: (*B*) *Oenothera nanella*, a dwarf form having 14 chromosomes (2 *n*) like the parent species, and (*C*) *Oenothera lata*, with 15 chromosomes (2 *n* + 1). Redrawn from De Vries.

381. Other Changes in Chromosome Number. Another mode of departure from the ordinary course of nuclear division consists in the failure of sister chromosomes (or, in the first reduction division, of the chromosomes of a pair) to separate and to pass to opposite poles. If both pass to the same pole, one daughter nucleus receives one more, the other daughter nucleus one less, than the usual number. If this occurs in the direct ancestry of spores or gametes, some of these reproductive cells

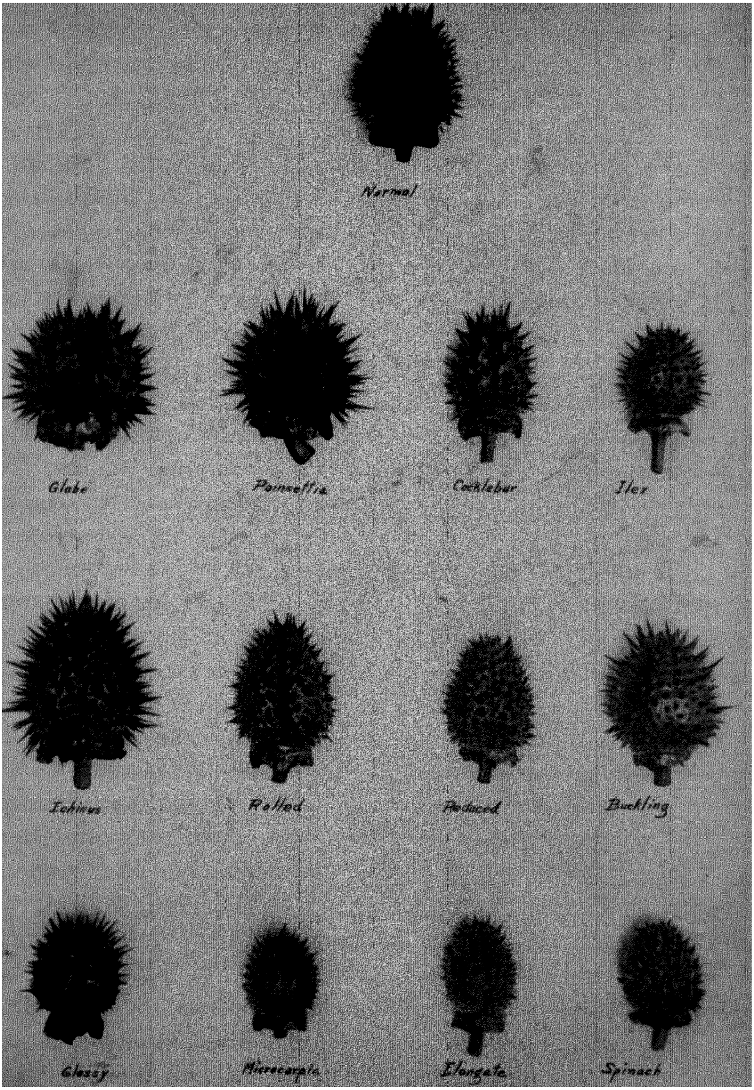


FIG. 402. Above, a fruit of the Jimson weed (*Datura Stramonium*), which has 24 chromosomes (2 n). Below, the fruits of 12 variant forms that have arisen from this species, each variant having 25 chromosomes (2 n + 1). After Blakeslee, in the *Journal of Heredity*.

will possess $n + 1$, others $n - 1$ chromosomes. If then a plant produces some gametes with each of these numbers, together with other gametes having n chromosomes, haphazard union of such diverse gametes might result in the appearance of offspring having variously $2n - 1$, $2n$, and $2n + 1$ chromosomes.

The evening primrose already referred to has produced a number of forms having 15 ($2n + 1$) chromosomes (Fig. 401, *C*). Fifteen-chromosome plants differ markedly from the parent form in such characters as form of leaf and habit of growth. Each such variant plant seems to have been produced by the union of a gamete with 7 (n) and one with 8 ($n + 1$) chromosomes. The Jimson weed (*Datura Stramonium*) also has given rise to a series of forms with $2n + 1$ (in this case 25) chromosomes (Fig. 402). In both of these as well as in other genera, the theoretically possible forms with $2n - 1$ chromosomes do not occur. Apparently gametes with $n - 1$ chromosomes do not function or, if they do, the resultant zygotes with $2n - 1$ chromosomes do not develop into new plants.

As a result of other irregularities in nuclear division more or less similar to that just described, many different chromosome groupings may arise. Evening primrose plants have appeared with chromosome numbers ranging from 7 (n) to 30 ($4n + 2$). A corresponding series in the Jimson weed runs from 12 (n) to 51 ($4n + 3$). Evidently many plants with variant chromosome numbers can not, for reasons already stated, perpetuate themselves. Others may do so. For example, if a plant has $2n + 2$ chromosomes, the two extra chromosomes representing the same pair, a regular pairing may conceivably occur and functional spores and gametes may be produced. There are genera whose species growing in the wild show series of chromosome numbers which may well have arisen in consequence of irregular behavior on the part of individual chromosomes. An example is *Carex* (the sedges), whose various species have such chromosome numbers as 30, 32, 36, 38, 48, 50, 52, and up to 112.

As to the causes which in nature modify the usual course of division, affecting either single chromosomes or chromosome sets, nothing is certainly known. There is evidence that high or low temperatures may play a part. Experimentally, the proportional occurrence of such irregularities has been increased by treatment with X-rays or with radium.

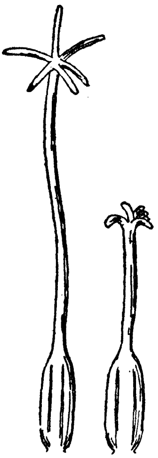
382. Changes Affecting Parts of Chromosomes. Apart from cases of unusual behavior of whole chromosomes, irregularities or accidents sometimes cause transverse breaks in chromosomes. Such breaks may take place during nuclear division, and also, apparently, at other times as well. They occur under natural as well as under cultural conditions. The proportion of their occurrence, like that of the deviations previously discussed, is increased by treatment with X-rays or radium.

A chromosome once broken, various fates may overtake its fragments. They may remain separate; in such a case one part is often lost; but apparently it sometimes persists, so increasing by one the chromosome number of the nucleus containing it and of the descendants of that nucleus. One fragment may be inverted and reattached to the other; or it may become attached to a different chromosome. If two breaks occur in one chromosome, the middle fragment may be inverted and reattached, or it may become separated and the end portions reunited. If breaks occur in two chromosomes, sometimes there is an exchange of segments and a reattachment in new combinations.

Varied effects upon inheritance result from changes such as these. The permanent loss of a part of a chromosome seems not necessarily to be fatal to the cells of the individual in which that loss occurs; but it may result in a failure to produce either functional gametes or functional zygotes. If, on the other hand, both or all fragments of a chromosome are retained, the consequence may be the appearance of a race with an increased chromosome number. It is possible that such a series of chromosome numbers as characterizes the sedges may have resulted in part from chromosome-fragmentation. An interchange of segments between two different chromosomes leads to changes in the arrangement of linkage groups, and to some degree of cross-sterility between the new form and the old. Such segmental interchanges have occurred in the establishment of races of certain plants, including corn and pea.

383. Changes in Nature of Genes. These, according to current views, explain the majority of cases of heritable variation. In many instances a red- or blue-flowered species has been observed to give rise to a white-flowered race. In Drosophila a red-eyed species occasionally produces individuals whose eyes are vermilion or white. The evening primrose has now and then produced a dwarf

plant (Fig. 401, *B*), and at other times a plant with especially short styles (Fig. 403). In such cases as these, if the new form is crossed with the parent form, the offspring show a distribution of the pair of characters concerned similar to that which appeared in Mendel's experiments. That is, the offspring behave as though the new race differed from the old in a single gene. It is assumed in each such case that a gene of the parent has become changed and that the change in the gene caused the appearance of the new character. It is assumed also that, when two races occurring in nature are crossed, if the character or characters that distinguish them are distributed among the offspring in a Mendelian fashion, then one of those races was derived from the other (or each from a common ancestor) in consequence of changes in one or more genes. As yet nothing is known about the factors which in nature cause such changes. It is known, however, that the proportion in which they occur can be increased by radiation (X-rays and radium) and by high temperatures.



A B

FIG. 403. Pistils of *Oenothera Lamarckiana* (*A*) and *Oenothera brevistylis* (*B*), the latter a variant form with short styles. Redrawn from De Vries.

Changes involving genes may conceivably consist in changes in the nature of old genes, in their complete loss, or in the appearance of entirely new genes. It is an interesting fact that in the experimental study of variation a great number of variations have been observed which can be explained as due to changes in, or loss of, genes, whereas comparatively few seem probably to have resulted from the appearance of new genes.

Changes in number of chromosomes and those due to the fragmentation of chromosomes can be directly observed. Changes in genes can not, since the genes themselves are too small to be seen. The occurrence of such changes, therefore, can only be inferred from the indirect evidence supplied by breeding experiments.

384. New Races Resulting from Variation. While individuals produced by the methods of heritable variation just discussed differ greatly in their ability to survive and reproduce, and in the constancy with which their characters are transmitted to offspring, many such variant plants and animals have proved vigorous and

capable of giving rise to offspring like themselves. Hence these methods of variation are likewise methods by which new, stable races arise. It is worth noting, however, that races coming into being in consequence of changes in the distribution of chromosomes or of parts of chromosomes possess characters which, however new in appearance, are the expression of previously existing genes now present in changed numbers, changed proportions, or changed combinations. Real progress in an evolutionary sense can apparently come about only through the development of new genes; and this, so far as can be seen at present, is a rare occurrence.

385. New Races Produced from Crosses. When a stable new race has appeared differing from its parent race in one or more genes, it will usually interbreed with the old race as well as with other new races derived from the same parent race. That is, crosses will occur, or can be brought about, between individuals differing with respect to one, two, or several pairs of genes. If two individuals differing in two or more pairs of genes are mated, their descendants in the F_2 generation, in consequence of recombinations of chromosomes and of crossing over between chromosomes, will possess varied combinations of grandparental genes. Among these combinations will be some that differ from the combination possessed by either grandparent. Individuals with these new combinations of genes will usually present new combinations of visible characters; and if they are able to live and to reproduce, they may give rise to new races.

Such production of new races by the crossing of related forms, making possible varieties with new combinations of desirable qualities, is largely used by plant and animal breeders. Many varieties of useful plants and animals have resulted from crosses between different varieties or different species—for example, numerous cultivated apples, potatoes, roses, and orchids. New races, varieties, and species are likewise constantly arising in nature from accidental crosses between related but distinct forms. In each case, whether in cultivation or in nature, the varieties or species to be crossed must previously have originated by variation from a common source. This method of producing new races likewise gives rise to no new genes; some of the old genes are combined in new ways.

CHAPTER XXXIII

EVOLUTION

386. The Facts of Evolution. In the preceding chapter was given a brief outline of what is now known regarding the ways in which new races and species of plants and animals come into existence. Observation shows that new races and species do thus appear from time to time, and that some of them increase in numbers and in the extent of territory occupied, and become established among older species. It is observed too that some older species are growing fewer in number of individuals and are occupying gradually smaller areas, and that from time to time a species disappears altogether. The plant and animal population of the earth is therefore constantly changing in consequence of the appearance of new species derived from older ones, of changes in the proportional numbers of different species and in the area they occupy, and of the disappearance of some of the older forms. This continuous process of change in the make-up of the earth's population is referred to as *evolution*, or *organic evolution.*

387. The Evolutionary Generalizations. The constant and gradual change in the population of the earth, now seen to be in progress, has been going on from as early a time as history and archeology record. The process is a slow one, and individual species may continue in existence for thousands or even millions of years. Nevertheless, the present condition of the earth's surface, as concerns the species of plants and animals inhabiting it and their distribution, is, taken as a whole, different from the condition that existed when the Egyptian pyramids were built, and still more widely different from that which prevailed in the days of the Crô-Magnons. Upon this well-established *fact* of constant change is based a *generalization* which says that a similar process of gradual change has been continuously in operation since living organisms first appeared upon the earth.

While the constancy of change in population over a very long period of time is established by direct evidence, it can not be directly demonstrated that new species which have appeared from

time to time have invariably descended from older species. Such an origin is absolutely shown for a new species only when the origin of that species is actually observed. However, the fact that new species are seen to arise from older ones, and the further fact that variation is universally characteristic of living organisms, have led to a second generalization, namely: that all species now living arose by descent from older species, those from still older ones, and so on back to the organisms that were first to inhabit the earth.

These two generalizations, supported as will be seen by an immense mass of evidence derived from many independent sources, constitute foundation stones of present-day thought. It was Darwin who first brought together much of the evidence in their favor. No one who, since the publication of his "Origin of Species" in 1859, has impartially investigated this evidence has questioned the validity or the usefulness of the idea of continuous evolution. But it must be remembered that the second generalization in particular is not itself, and probably never can become, an established fact. While all the available evidence tends to confirm the conception, it can not be absolutely proved that all species have arisen, as species are now seen to arise, by descent from older species.

The evidence upon which these important generalizations are based is of six general sorts: the observed origin of new races; the facts of classification; the facts of underlying similarity in structure; the facts of similarity in function and development; the facts of geographic distribution; and the fossil record of extinct species. Of these six classes of evidence, the first-mentioned has been sufficiently discussed.

388. Evidence from Classification. When a considerable bulk of information accumulates upon any subject, it becomes necessary to classify that information in order that it may readily be utilized. The Greek and Roman observers who, so far as is known, were the first to preserve in writing extended observations upon plants, saw that many individuals possess much the same characteristics; they grouped together all the plants that seemed to them substantially alike under one name. So arose the conception of *species*, each species including many individuals. As the number of known species increased, those which seemed more or less alike were grouped together in such larger units as are nowadays called genera and families. The first classifications of this nature

were *artificial.* The classification of Linnaeus, published in 1753, which was by far the most important up to its time, was strictly artificial; it was based, so far as seed plants were concerned, primarily upon the number of stamens in the flower of each species.

As knowledge of plants increased, it was seen more and more clearly that species fall naturally into larger groups, the similarity between the species within any group being indicated, not by one character alone such as number of stamens, but by many characters of flowers, fruits, and vegetative parts. Most classifications since Linnaeus' time have attempted to take into consideration these numerous similarities between species; present-day classifications are, therefore, as far as available information permits, *natural* instead of artificial. A natural classification expresses the fact that some species are so closely similar that they belong together in a group called a genus; that several genera, while showing somewhat wider differences than those between closely related species, are sufficiently alike to be grouped in a family; and, likewise, that related families belong together in an order, related orders in a class, and related classes in a division. A natural classification is an expression of various degrees of likeness that actually exist among plants. Among species of animals, also, varying degrees of similarity appear, and the classification of animals like that of plants has progressed from the stage of an artificial to that of a natural system.

It seems impossible to explain the occurrence of such a scale of similarities between species except by supposing that each degree of similarity represents a comparable degree of relationship. Relationship implies that all the species of a genus are descended from a single species, that all the genera of a family are descended from a single but more remote source, and so on for the origin each from a single source of the families of an order, the orders of a class, and the classes of a division.

389. Evidence from Structure. The classification of plants and of animals is based in the main upon details of structure; but in classifying, ordinarily only those structural features are taken into account which are found especially useful in making the classification. When, however, a study is made of all the elements that enter into the structure of particular species, further evidence appears as to the relationships between species, and more especially between larger groups. For instance, the presence of leaves

borne on a stem belonging to the sporophytic generation is a character practically universal throughout pteridophytes and seed plants. Although leaves show the greatest diversity in form and function—for example, foliage and scale leaves, spines and tendrils—their manner of origin and their development show them to be all of fundamentally the same nature. A like statement may be made of the various forms presented by stems and by roots. That is, the same general plan of structure characterizes the sporophytes of all the species that are grouped together as pteridophytes and seed plants. The universality of a general plan of structure throughout these two divisions seems explainable only by supposing that all pteridophytes and seed plants are descended from a common ancestry.

Confirmatory evidence is afforded by the occurrence of strobili of similar general plan in various orders of gymnosperms, and of flowers, likewise of similar general plan, throughout the angiosperms; and, among internal structures, by general likeness in the vascular systems of pteridophytes and seed plants. The presence of archegonia, again of the same general plan, in all bryophytes and pteridophytes points, with other similarities in the gametophytic generation, to a relationship between the members of these two divisions. Perhaps the most far-reaching evidence of relationship is offered by the regular recurrence of flagellate cells, in the form of swarm-spores in algae and fungi, and in that of gametes, especially male gametes, in algae, fungi, bryophytes, pteridophytes, and the more primitive seed plants (such as Zamia). The widespread power of forming flagellate cells seems to point to the descent of the plants of all these groups from flagellates.

390. Evidence from Similarity in Function and Development. The study of the functions of plants, like the study of their structure, shows likenesses in important respects between the members of each major group, as well as similarities of less fundamental character within the limits of smaller groups. Indeed, certain characteristics are common to all living organisms, such as the essential structure of living matter itself and its organization into cells, the power of responding in varied ways to stimuli of many sorts, and the ability to carry on both constructive and destructive metabolism. The universal possession by all plants and animals of these powers and characteristics unavoidably suggests their descent from a common ancestry. On the other hand, many func-

tions are peculiar to, or especially characteristic of, certain groups and, taken together with other similarities, indicate a relationship between the members of each such group. The plants of some groups form cell walls largely by the secretion of cellulose; those of other groups, by the secretion of chitin. The typical reserve food manufactured by the organisms of some groups is a sugar; in other groups it is starch; in others, glycogen; in still others, a fat. An illustration of a function characteristic of a relatively small group of plants is furnished by members of the pulse family; the reserve foods which most of them store in largest amount in their seeds are proteins, whereas starch is the most abundant reserve food in the seeds of most other families of angiosperms.

The light thrown upon evolution by the development of individual organisms may be considered with that supplied by other functions, since development is itself a function of the developing organism. The history of all many-celled plants and animals is alike in that each individual begins its existence as a single cell, and that its development to maturity consists in a series of cell divisions together with an increasing differentiation of cells into what are, in the more complex species, tissues and organs. In addition to this general resemblance between all organisms, more detailed similarities appear in the development of individuals of separate divisions, classes, and orders. For instance, the seedlings of most if not all conifers bear needle-like leaves on long branches; although mature plants of different species, such as pines and arbor vitae, differ greatly in the form and arrangement of their leaves. The structure of the embryonic sporophyte of the bracken, consisting of root, leaf, foot, and stem, is characteristic of the corresponding stage in the sporophytic development of most other ferns. Other pteridophytes, such as Equisetum and the club mosses, have embryos similar to that of the bracken in general plan, although differing in important respects. The differences indicate a more remote relationship between Equisetum, club mosses, and ferns than that among the ferns themselves. As has been seen, dicotyledons and monocotyledons are distinguished in several ways which indicate that these two classes of angiosperms have long been separate.

391. Evidence from Geographic Distribution. The distribution of plants also furnishes much evidence as to relationships between species as well as between genera, families, and orders. In general,

where a large area of land exists, sufficiently uniform as to climate and soil and not broken by barriers which interfere with the migration of plants, its native flora is likewise uniform; that is, its whole extent is inhabited by the same or closely similar species. Instances of such large areas in North America occupied by uniform floras are to be found in the tundra, the northern evergreen forest, and other regions to be described in the following chapter. On the other hand, if an effective barrier exists, such as a high mountain range, an extensive desert, or a large body of water, the floras on opposite sides of the barrier are likely to be very different. For example, the flora of the region west of the Rocky Mountains differs greatly from that of the region to the east. Much of this difference, to be sure, is due to climatic differences; but when, as is frequently the case, two species of the same genus occur on opposite sides of the mountains, they are usually so different as to suggest that they have been separated and have undergone evolutionary changes in divergent directions during a considerable time. The flora of Madagascar and that of the neighboring coast of Africa are very distinct. Marked differences exist also between the floras of Australia and of the Asiatic mainland.

The degrees of similarity or difference between the floras of separate bodies of land, such as islands or continents, furnish indications as to whether or not such land areas were at one time connected; and conclusions upon such points, based upon the characteristics of floras, agree in general with conclusions founded upon geological study. There is sufficient likeness between the floras of eastern North America and western Europe—although the native species of these regions are as a rule distinct—to render it probable that at a not very distant geological period the two continents were connected by land that has now disappeared.

392. Evidence from the Fossil Record. In the sedimentary rocks—which were formed from deposits at the bottoms of bodies of water in past ages—are many remains of plant parts. Some of these remains are impressions or casts, which show only the general form and the surface structure of the plants or organs that formed them. Others are petrifactions, resulting from the gradual replacement of the materials of plant bodies by mineral substances deposited from a solution with which the plants or plant parts were impregnated. Sections of a petrifaction show much of the original structure of the plant, often to minute microscopic details.

Necessarily, fossils, with rare exceptions, show only broken, often partly decayed, fragments of plants. The softer plants, such as algae and mosses, are less often preserved than are harder, more woody plants or those with silicified cell walls. In the time that has elapsed since fossil-bearing rocks were formed, these rocks have been subjected to great changes in consequence especially of heat and pressure; and in the course of such changes many of the fossils present were destroyed. For all these reasons, the fossil record of ancient plants is very fragmentary, with many large gaps which laborious investigation is but slowly closing.

In spite of its incompleteness, however, the fossil record supplies much information regarding the nature of plants of past times. The evidence so obtained as to the general course of evolution agrees with that furnished by the structure and functions of living plants. The distribution of fossils through rocks of different ages indicates, for example, that the earliest plants were comparatively simple water-inhabiting species. In later ages appeared pteridophytes, primitive seed plants, forms more or less similar to present-day gymnosperms, and finally angiosperms.

393. General Course of Evolution. Six classes of evidence have now been cited as indicating that evolution has been a continuous process from the first appearance of living organisms upon the earth. All this evidence, except that belonging in the first category (the observed origin of new races) agrees in indicating that the course of evolution has been in general, though with many exceptions, from simplicity to complexity. Primitive organisms seem to have been very simple, and larger and more complex ones to have come into existence step by step. So strongly is this conception of the course of evolution supported by the available facts that it is virtually unquestioned. The series of types described in previous chapters, leading from Chlamydomonas to angiosperms, illustrates the accepted notion as to the general course that the evolution of plants has followed.

This conception implies that from time to time heritable variations have occurred, each of which introduced a new character or a new group of characters. But it is notable that, so far as the actual origin of new races is now observed, such a race seems to arise in the great majority of cases in consequence of a recombination of genes already existing, or as a result of a change in or loss of a gene. Only in rare cases is a new race observed to arise

apparently because of the acquisition of a new gene. It is true, because of the complicated interrelations between genes and characters (§ 375), that a new combination of genes, or even at times perhaps the loss of a gene, may result in the appearance of what must be considered a new character. Nevertheless, the progressive evolution of new species possessed of new possibilities would seem to have meant the acquisition from time to time of new genes. The seeming discrepancy between the general course that evolution appears to have followed in the past and the course that it is observed to be following at present is not to be overlooked. This discrepancy may perhaps be explained by the consideration that the progress of evolution has been extremely slow. Even the rare development of new genes may, in the course of the hundreds of millions or billions of years during which organic evolution has been going on, have brought into existence the diversified forms of plants and animals that now populate the earth.

394. Survival and Extinction of Races. The evidence just outlined indicates that, as new forms are now coming into being, so new races and species have arisen in the past. Of the plant and animal forms that have originated by variation, some have been very short-lived; some have become well-established species which persisted during long periods, although the great majority of species that lived in previous ages sooner or later disappeared. Evolution—the progressive change in the sum total of organisms inhabiting the earth—depends not only upon the appearance of new races as a result of variation, but also upon the relative ability of new as well as of older races to perpetuate themselves.

Whether or not a race shall persist, and if it does, how widely it shall become distributed, depends upon the interaction of many factors. These factors may be classed under four heads: the ability of the race to reproduce; the degree of its adjustment to the non-living environment; conflict of interests with other organisms; and coöperation with other organisms.

395. Power of Reproduction. Reproduction includes all means by which the number of individuals of a species may be increased; among them, cell division in one-celled organisms; in many-celled organisms, the formation of spores and other special reproductive bodies, gametic union, and varied methods of vegetative multiplication. Other things being equal, a species which multiplies rapidly is more likely to survive and spread than is one which multiplies

slowly. The great success of weeds like the dandelion and Canada thistle is largely a result of their remarkable powers of reproduction. Rapid multiplication is especially important to such saprophytic plants as the bread mold, or to parasitic plants like the wheat rust. Both are dependent upon the more or less accidental and temporary presence of the necessary substrate or host; and both produce immense numbers of spores, so increasing the chance that some spores may reach the host or substrate.

396. Adjustment to the Non-living Environment. An organism is dependent for existence upon the conditions surrounding it. If it lives in water, it must be able to secure from the water the substances essential to its metabolic processes. If, like most seed plants, it lives partly in the soil and partly in the air, its structure must enable it to secure from these two sources the necessary materials, such as carbon dioxide, oxygen, water, and inorganic salts, and must prevent the loss of water at a more rapid rate than that at which it can be obtained. If surrounding conditions are subject to periodic changes, the organism must be able to pass into stages in which its functions or structure, or both, are modified to correspond with the changes in environment. Thus Spirogyra, which often lives in ponds that become dry in summer, forms zygotes that can endure drying and can germinate when water is again present. Any perennial seed plant of a temperate or cold region has means of preserving alive through the winter, though in a dormant condition, either its whole body (as an evergreen tree) or a part (such as a tuber or underground stem) and of resuming vegetative activity upon the return of warmer weather.

Now and then the environment changes in a way that affects all plants and animals over a large area. A low region is uplifted, becoming drier and perhaps colder; or marked climatic changes occur, such as led to the glacial period in the northern hemisphere, and later to the disappearance of glaciers and the restoration of a milder climate over large parts of Europe and North America. Such changes on a large scale profoundly affect the course of plant and animal evolution. Among the older organisms of the region, only those survive that are adjusted to the new conditions; and among new forms that may result from variation, especial opportunities are offered, because of the disappearance of many older species, to those whose structure and functions fit them to the changed environment.

397. Conflict of Interests. The interests of different individuals of the same or of different species come into conflict in a variety of ways. In general, as Darwin long ago pointed out, most species can give rise by reproduction to vastly more individuals than the available supply of foods could support. An illustration of such a possibility in the case of bacteria was given in § 189. While bacteria reproduce more rapidly than do most other organisms, the same general principle applies to most species of plants and animals. Consequently, there occurs among the individuals of each species a competition for food materials; and those individuals that are best adapted by length of root, rapidity of growth, power of absorption, or in any one of many ways to succeed in obtaining nutrients are those which will survive and will in turn produce offspring. In so far as the advantages possessed by such individuals are heritable, their offspring will possess the same favorable characteristics. In this way the competition for food materials tends to *select* those strains within a species that are best fitted to secure nourishment, and so to improve the average of the species in this respect. Just as does a competition for food materials, so a competition for favorable conditions, such as a temperature suitable for growth, results from the presence of an increasing population. In various respects, therefore, the tendency to overpopulation brings about, through competition, an improvement in the average capacity of each species to maintain itself. Similarly, there is competition between different species for food materials and other necessities. The net result of the crowding of population and of the consequent competition is to select those species, and those strains or races within each species, that are best fitted to maintain themselves under the conditions surrounding them.

The survival of strains, races, and species is affected by other forms of conflict which are not so obviously competitive. One is the preying of some organisms upon others; a particular form of this is parasitism. The relations between a parasitic fungus and its host plant favor, on the side of the parasite, those individuals best fitted to secure nourishment from the host; and on the side of the host, those individuals that are most effectively guarded from the attacks of the parasite, or that can best survive the injuries which the parasite inflicts. Another illustration of conflict is that between the human species and weeds. Weeds conflict with man's practical interests when they interfere with the grow-

ing of crops; and with his esthetic interests when they deface lawns and parks.

398. Coöperation. Competition as an evolutionary factor is much discussed. Not so much is ordinarily said of the bearing upon evolution of coöperation between individuals of the same or of different species. Yet the part played by coöperation in evolutionary development has perhaps been fully as great as that played by competition. Among very primitive organisms, coöperation is illustrated by the tendency in many lines of descent for one-celled organisms to come together or to remain together in colonies. Further steps in coöperation were taken when different cells of the same colony took on different functions and became differentiated in structure; this differentiation finally leading to the development of tissues. As between more complex plants and animals of the same or of different species, there are innumerable illustrations of the tendency to coöperate. One type of coöperation is the establishment of a partnership, as between a leguminous plant and the bacteria in the nodules of its roots; between forest trees and the fungi whose mycelia become closely associated with their roots; or between the fungus and the alga in a lichen. Another type of coöperation is seen in the formation of plant associations, illustrated by the relations between forest trees and the shrubs and herbaceous plants that grow in their shade. Another is illustrated by insect pollination and the accompanying interrelations between angiosperms and insects; still another by the cultivation by man of useful and desirable plants and animals. A very extensive piece of coöperation is involved in the nitrogen cycle (§ 197), participated in by most of the many-celled plants and animals, some of the higher fungi, and many bacteria.

399. Natural Selection. The factors belonging to the three classes last mentioned may be grouped together as involving the relations between an organism and its environment; since the environment of any individual includes the other organisms, as well as the non-living things, with which it comes in contact. The effect of all these environmental factors, taken together, upon the course of evolution is often referred to as "natural selection," because the net result of the influences at work is to preserve or select those individuals, races, and species that are best adapted to the environment. Differences in power of reproduction between different species may tend to the perpetuation and extension of a

species which is also favored by natural selection. On the other hand, it may and often does happen that these two sets of selective factors (natural selection and differential powers of reproduction) work in opposite directions; so that a species that is favored by its powers of rapid reproduction is discriminated against by natural selection, or *vice versa.* Much the same idea as that involved in natural selection, but with emphasis upon the competitive factors, is expressed by the phrase "struggle for existence." The term "artificial selection" is sometimes applied to the conscious selection of desirable races by man. But since man is one of the species that constitute a part of the environment of other species, the distinction between natural and artificial selection is meaningless.

CHAPTER XXXIV

THE GEOGRAPHIC DISTRIBUTION OF PLANTS IN NORTH AMERICA

400. Factors Concerned in Distribution. Under natural conditions the distribution of plants over a given area is governed by a complex of factors which are in part hereditary and in part environmental. The nature of the hereditary factors, which affect in very important ways the ability of a plant to live in a particular environment, has been discussed in Chapter XXXII. The environmental factors fall naturally into two groups: those related

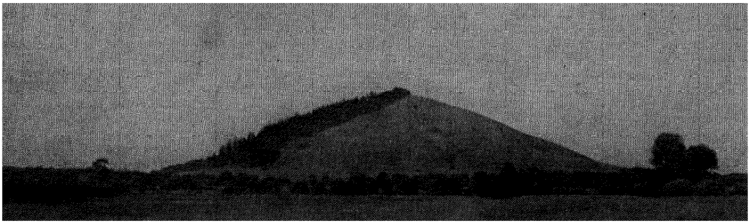


FIG. 404. Relation of soil moisture to the distribution of vegetation. The portion of the hill at the right is exposed to drying summer winds. The soil of the sheltered northern slope at the left retains sufficient moisture to permit the growth of a forest.

to climate, such as temperature, moisture, light, and wind; and those related to the soil, including its physical make-up, its chemical composition, its slope and drainage, and the amount of available water.

The hereditary endowment of some plants is such that they can become adapted to a wide range of habitats. The common dandelion, for example, thrives on a great variety of soils and ranges from lowlands to mountain tops. Most plants, however, can not become adapted to so wide a range of conditions; their distribution, therefore, is dependent upon a more definite set of factors, the absence of any one of which from the environment makes the existence of the plant in that habitat impossible. Many species

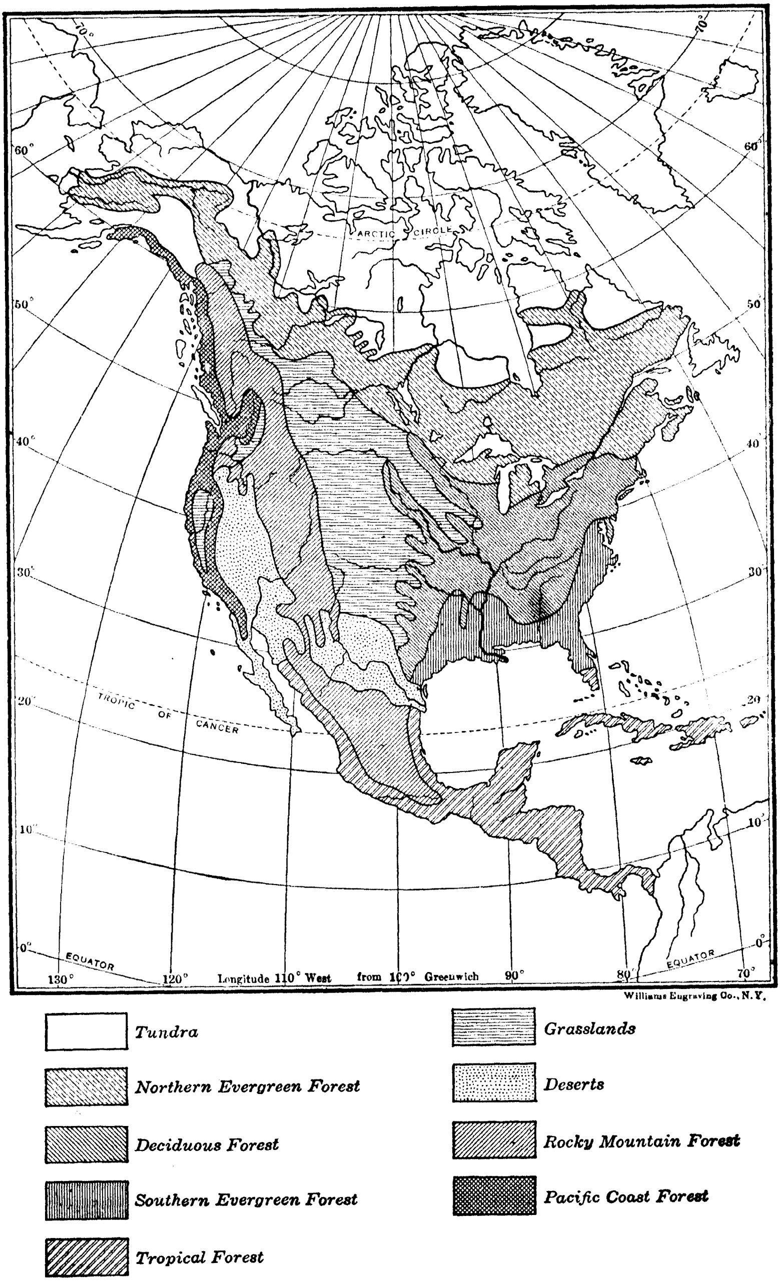


FIG. 405. General regions of vegetation in North America.

of tropical or subtropical plants, such as palms, oranges, lemons, and bananas, are badly injured or killed by freezing temperatures. Cacti, growing best on arid soils, are unable to live in wet, poorly aërated soils. Cranberries find their natural habitat in acid bogs and die quickly if transferred to neutral or slightly alkaline soil. Seedlings of hemlock grow best in dense shade, but those of some poplars require abundant light for growth and development.

401. General Regions of Vegetation. In consequence of the interaction of the various factors concerned in the distribution of

FIG. 406. The tundra.

plants, North America may be divided roughly into four regions of vegetation: tundra, forests, grasslands, and deserts. Each of these general regions is of course capable of further division and subdivision. In the following discussion the boundaries of the respective regions are given only in a general way, since they merge one into another, often with broad transitional zones; and the brief descriptions are of the vegetation as it existed before the extensive settlement of the continent. In the United States, particularly, man has destroyed or profoundly modified much of the native vegetation.

402. Tundra. The tundra, in general, fringes the northern limits of the continent from Alaska to Labrador. Here the winters are long and cold, with relatively light snowfall. The air in winter is very dry, and often strong winds blow. The growing

season is of short duration. Only the upper portion of the soil thaws, to a depth of from a few inches to one or more feet, this depth varying chiefly with the direction of the slope; consequently the soil temperature is low and the ground water is cold. The plants that are able to thrive under these conditions include certain mosses, lichens, grasses, and sedges, a few other herbs, and some shrubs. Many of the herbaceous species bear relatively large and brightly colored flowers, although their stems are for the most part very short so that they form rosettes or compact cushions. The shrubs of the tundra are likewise characteristically low; there are several species of willow that grow to only a few inches in height.

403. Northern Evergreen Forest. In general, the northern evergreen forest stretches across the continent from the Atlantic to the Pacific. Its southern boundary extends from Vermont westward to the Great Lakes and, including the northern portions of Michigan, Wisconsin, and Minnesota, swings sharply northwest to the eastern slopes of the Rocky Mountains. Thence it extends northward to Alaska. A wide transitional belt of mixed type joins the tundra with the densely forested area. In this belt forests fringe the rivers, but over large areas trees are scattered singly or in small groups. The dense forest is composed for the most part of conifers. Among them are black spruce, white spruce, balsam fir, tamarack, arbor vitae, hemlock, white pine, red ("Norway") pine, and jack pine. Deciduous trees (belonging to the angiosperms) occur among the conifers, and, especially where the original forest has been removed by cutting or burning, deciduous trees may form extensive pure stands. Prominent among them are the aspen, white birch, and balsam poplar.

404. Deciduous Forest. Merging on the north with the evergreen forest, the deciduous forest occupies an area extending approximately from central New York southwest along the Appalachians to Louisiana and Texas, its western boundary stretching from eastern Oklahoma to southern Wisconsin. This forest reaches its most characteristic development in the mountainous area of western North Carolina and eastern Tennessee. Among the common trees of this area are the white oak, black oak, scarlet oak, shagbark hickory, pignut hickory, sugar maple, red maple, chestnut, birch, ash, elm, walnut, and tulip tree. Associated with some of the deciduous trees, conifers such as the short-leaf pine,

white pine, and hemlock occur in the mountainous regions or on high hills. Rhododendron and various other shrubby plants often form extensive undergrowths on the mountain sides.

405. Southern Evergreen Forest. This forest area covers the coastal plains from eastern Virginia to Texas. The low, rolling,

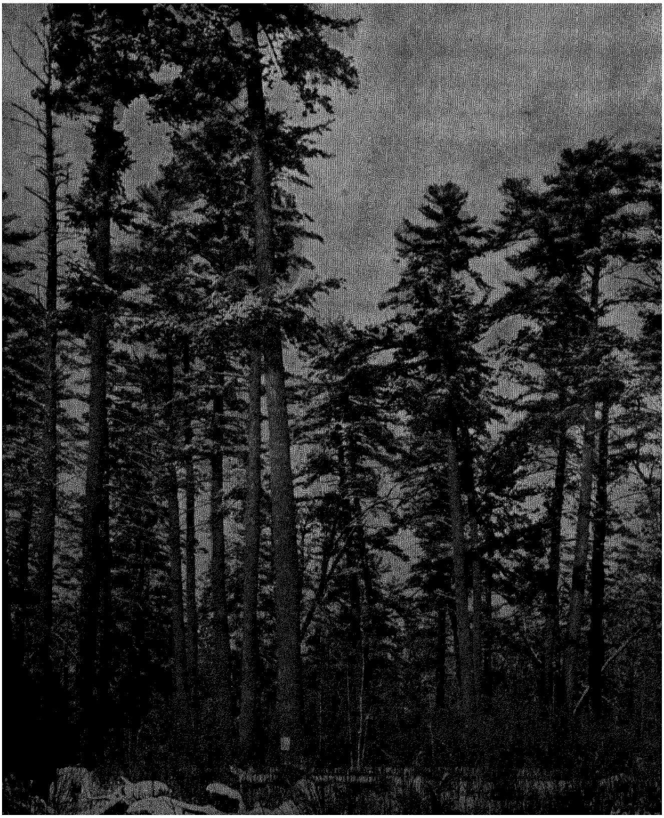


FIG. 407. A stand of white pine in the northern evergreen forest. After Moon and Brown.

sandy land near the coast from South Carolina to Louisiana is the habitat of the long-leaf pine. In and about the numerous and extensive swamps are live oaks, water oaks, bald cypress, gums, and magnolias. These trees are often heavily draped with an epiphytic seed plant, Tillandsia, commonly called "gray moss" or "Florida

moss." On the higher portions of the coastal plain, and more remote from the sea, are areas of short-leaf pine which merge into the deciduous forest of the Appalachian foothills.

406. Tropical Forest. The tropical-forest area includes the southern quarter of the peninsula of Florida, most of the coastal margin of Mexico, all of Central America, and the islands of the West Indies. The type of tropical forest developed in southern Florida is meager, but the tropical-forest relationship is shown

FIG. 408. A deciduous forest. Photograph by E. J. Kraus.

by various palms and other tropical trees, by lianas (climbing woody vines, Fig. 409), and by tropical epiphytes such as bromeliads and orchids. Along the coast, and fringing the keys, are characteristic mangrove swamps such as are usually found on muddy tropical shores.

The broad coastal plain of Mexico, except for the dry northwestern portion, contains grassy savannas, broken by jungle; but the southern portion, in consequence of its warm, moist climate, possesses a luxurious tropical forest. Such a forest in its fullest development is remarkable for the great abundance and variety of its flora and fauna. Commonly the tall trees form so dense a

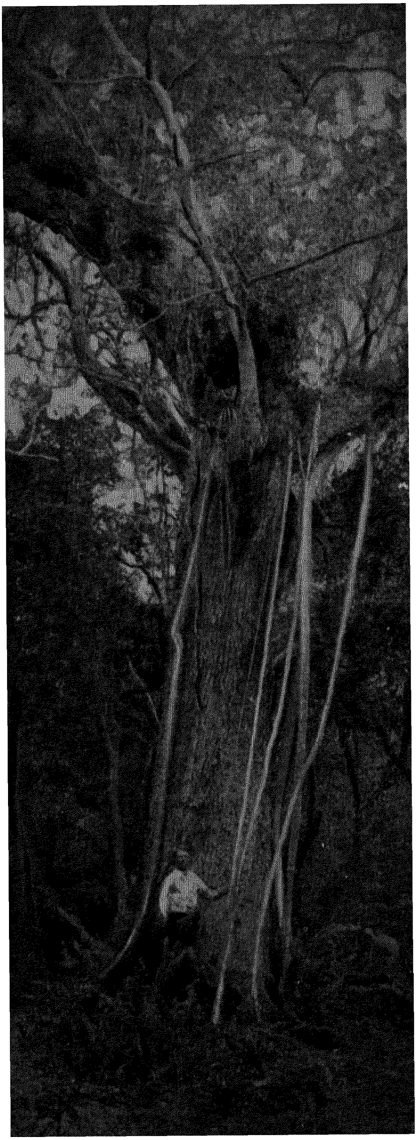


FIG. 409. A liana-covered tree in the tropical forest of Florida. Photograph by E. J. Kraus.

canopy as to shut off much of the light from the floor of the forest, resulting in a sparse undergrowth and making the forest open and easily penetrable. The trunks and upper branches of the trees, however, are heavily populated with a great variety of epiphytes —lichens, mosses, ferns, orchids, bromeliads, and shrubs. Lianas also are numerous, twining about the trunks of trees and pushing their tangled branches into the forest canopy.

In Central America and the West Indies much of the open forest has been destroyed by centuries of nomadic agriculture, and in its place, over large districts, has grown up a dense and almost impenetrable jungle.

407. Grasslands. This great area, whose eastern boundary extends irregularly from central Texas to southern Manitoba, includes the southern portions of Saskatchewan and Alberta and has its western limits along the foothills of the Rockies from Alberta to New Mexico. The name "prairie" is applied to the easternmost irregular strip of this grassland, reaching

from Texas to Manitoba. The prairie region was formerly covered with a rich growth of various kinds of tall grasses, forming a characteristically dense turf. Growing with the grasses were many other herbaceous plants, such as blazing star, asters, golden-rods, and sunflowers. In general, the soil of the prairie is rich in humus, beneath which lies clay or sand. The nature of the soil seems, however, to have played little part in determining the absence of trees in this region. The treelessness of the prairie has been variously accounted for, having been ascribed, for example, to frequent and extensive fires or to the grazing of vast herds of buffalo. Whatever minor part tnese factors may have played, it is probable that the prairie has remained treeless chiefly in consequence of an excessive transpiration in proportion to the amount of soil water available for the use of plants.

That extensive area of the grasslands which lies west of the prairie constitutes the "Great Plains" and is the home of grasses which are characteristically short and grow in patches or tufts. Scattered over the Great Plains also are various cacti as well as other herbs and shrubs adapted to dry habitats. The western margin of the plains passes into various types of scrub growth. Climatic conditions apparently are responsible for the characteristic vegetation of the plains. The light annual rainfall and the high rate of transpiration seem to make the development and growth of tree seedlings impossible under natural conditions.

408. Deserts. The area extending south from eastern Oregon and western Idaho, embracing most of Nevada and Arizona, the southern portions of California and New Mexico, and including a part of southern Texas and northern Mexico adjacent to the Rio Grande, is largely made up of desert areas. Most of the peninsula of Lower California also is desert. This whole region is in general one of low rainfall and high evaporation.

The extensive depression between the Sierras and the Rocky Mountains, often called the "Great Basin," is dominated by the sagebrush, a dusty-gray shrub with strongly scented leaves. Associated with sagebrush are a few other shrubs of similar appearance. After the seasonal rains appears a sudden growth of small annual plants which flower and fruit and as quickly wither and disappear. The appearance of the desert therefore varies greatly with the time of year.

To the south and southeast the Great Basin passes into a region

of intense summer heat and scanty rainfall. Here is a remarkable development of plants peculiarly adapted to an arid habitat. The leafless creosote bush, cacti (Fig. 411) of weird shapes, yuccas (Fig. 50), and thick-leaved agaves are among the characteristic plants of this region. Bunch grasses are found in certain areas,

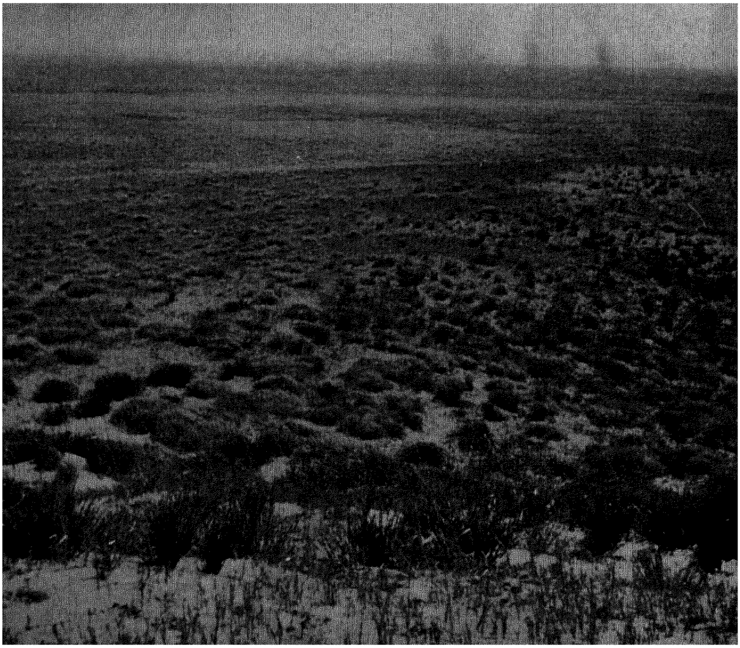


FIG. 410. Vegetation of the semi-arid sand hills of eastern Colorado. The dominant plant of this region is the sagebrush (Artemisia). After Duggar (photograph by H. L. Shantz).

and after the seasonal rains annual grasses and other small herbs appear.

409. Western Evergreen Forest. The western evergreen forest extends in general from Alaska to southern Mexico, and may be divided roughly into two areas: the Rocky Mountain forest and the Pacific Coast forest. Conifers are the chief forest trees in both areas.

The Rocky Mountain forest stretches along the Rockies from northern British Columbia to southern Mexico. This great system of mountains, extending nearly the whole length of North

America, presents a wide range of climates which vary with the latitude, as well as with the elevations at any given latitude. In consequence of the diverse climatic conditions, not all of this great mountain area is covered with forests. Thus, within the United States, the eastern slopes of the Rockies, grading into the more or less arid plains, have a general level below which trees do not grow. This level lies roughly between 4,000 and 6,000 feet.

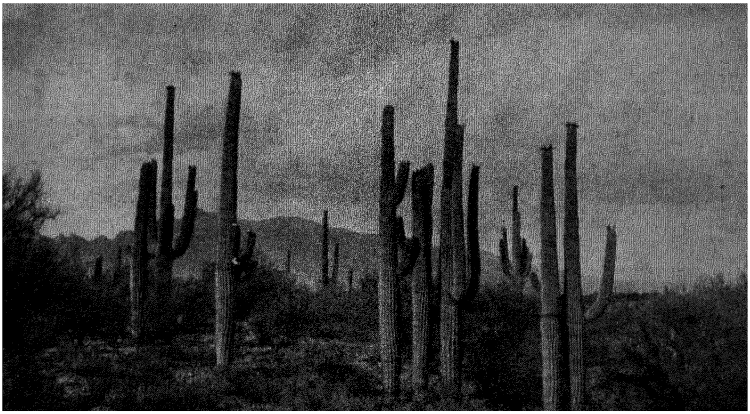


FIG. 411. A desert region of Arizona, showing "giant cacti" (*Carnegiea gigantea*). Photograph by Frank N. Campbell.

There is likewise a general level (the "timber line") above which trees do not grow. The height of the timber line also varies in different localities; in the Rockies of the United States it ranges approximately from 9,000 to 11,000 feet. Above this timber line a low "alpine" vegetation occurs, resembling that of the tundra. Farther and farther north along the mountains, both alpine and forest belts appear at increasingly lower levels; consequently, in the Canadian Rockies the forests cover the lower mountain sides and the valleys.

The dominant tree of the Rocky Mountain forest is the western yellow pine. The lodgepole pine also is widely distributed. Among other conifers are some of the true firs, the Douglas fir, the western larch, and the western hemlock.

The Pacific Coast forest occupies the slopes of the coastal mountains from southern Alaska into California. The area from Alaska to southern British Columbia is dominated by the Sitka spruce.

With this spruce occur other conifers, among them the western hemlock and Douglas fir. The coastal region of southern British Columbia, Washington, and Oregon has a mild winter climate and a heavy annual rainfall. Because of these favorable conditions the

FIG. 412. The dense growth of trees characteristic of the western evergreen forest in Oregon.

conifers here reach a luxuriance unequaled in any other part of the world. Many of them grow to heights of 200 feet or more, and the bases of their trunks often exceed 10 feet in diameter. Douglas fir and western hemlock dominate among the large species; associated with them are other conifers such as the western white pine, Sitka spruce, white fir, and western white cedar. As a rule, the forest can be penetrated only with difficulty on account of the dense undergrowth of ferns, shrubs, and low-growing deciduous trees, including maples, poplars, alders, and birches.

On the coastal range, and confined to a narrow belt extending from the southern edge of Oregon into central California, are the coast redwoods (*Sequoia sempervirens*). Their even larger relatives, the "big trees" (*Sequoia gigantea*, Fig. 56), occur only in a few groves on the west slopes of the Sierras in central California.

CHAPTER XXXV

THE ECONOMIC SIGNIFICANCE OF PLANTS

Crop Plants

410. Why Plants Are Cultivated. The cultivation of plants for food and for other useful purposes has been carried on since very early times. The domestication of plants has been an important factor in the progress of the human race. When and by whom wild plants were first brought under cultivation, and when their selection and improvement began to give rise to the forms now chiefly cultivated, are not certainly known. Many common vegetables, fruits, and cereals have been cultivated for hundreds, and some for thousands, of years. It is known that rice has been grown for at least 5,000 years. The plants most largely cultivated for food by the ancients were those that produced edible seeds and fruits, particularly the cereal grains, leguminous plants, the apple, peach, fig, date, and olive. The cabbage and onion also have long been grown. Other plants, such as flax and hemp, were cultivated for their fibers; some as sources of dyes; and still others, like the tea and the grape, for use in the preparation of beverages. The majority of the plants more recently brought under cultivation are of less economic importance than those longer known, being used mainly for stock feeding or for medicinal purposes. The discovery of America and increased facilities for transportation and communication between the peoples of the world resulted in a more extensive use and distribution of existing varieties. Among the contributions of the Americas to the world's stock of cultivated plants were the Indian corn, the true beans, the potato, tomato, and tobacco. Many valuable new races and varieties of species previously cultivated have been developed, and efforts are constantly being made to modify and improve existing varieties, especially with a view to increasing the yield of their useful parts. Great changes in various organs of plants are brought about by selection, particularly in roots, leaves, and flowers. With few exceptions crop plants are seed plants, and the vast majority are angiosperms.

411. Organs Used for Food. Various parts of plants are sources of food. Even different plants belonging to the same family may be grown for the food found in different organs. In the goosefoot family, the beet and the mangel are cultivated for the food stored in their fleshy roots whereas chard and spinach are grown for their leaves. Some members of the mustard family, including the radish, turnip, and rutabaga, store food in enlarged roots. Others of the same family, such as white and black mustard, produce useful seeds. Many representatives of the pulse family, including the pea, bean, lentil, and vetch, are cultivated for their seeds; others, such as alfalfa and clover, are important forage plants. Although the grass family supplies the cereal grains, many other grasses, some wild and some cultivated, are used for forage. The underground branches (tubers) of the potato are used for food; in the same family, the eggplant, tomato, and peppers bear edible fruits, and tobacco is extensively cultivated for its leaves.

FIG. 413. The wild *Brassica oleracea* (*a*), from which the following cultivated plants seem to have been derived: (*b*) kohlrabi; (*c*) cauliflower; (*d*) cabbage; (*e*) Welsh or Savoy cabbage; (*f*) Brussels sprouts. After Smalian.

Equally marked differences appear between varieties of the same species. Thus the edible parts of the common cabbage and of Brussels sprouts are buds; kale is grown for its leaves; kohlrabi for its enlarged fleshy stem; and the cauliflower which, like kohlrabi and kale, belongs to the same species as the cabbage, is grown for its abortive flower clusters.

412. Other Uses of Plants. Apart from being cultivated as sources of food for man and domestic animals, many plants are grown or used for other purposes. Practically all the great variety

of beverages, aside from water and milk, are derived from plants; among them various fruit juices and alcoholic drinks, coffee, tea, chocolate, and cocoa. Many plants supply stimulating or narcotic substances, such as tobacco, opium, morphine, and cocaine. Fats and oils stored in fruits and seeds are of great commercial value, many of them being used in soap-making and for various other purposes. Olive oil, cottonseed oil, peanut oil, corn oil, and coconut oil are used for human food. Linseed oil, obtained from flaxseed, enters into the manufacture of paints, varnishes, linoleum, and printers' ink. Many waxes, gums, and resins, such as Japan wax, gum arabic, gum tragacanth, balsam, and turpentine, are plant products of commercial value. Other products obtained from plants include spices, flavors, perfumes, and many medicinal substances.

All the important textile materials, with the exceptions of silk, wool, and asbestos, are made from fibers derived from plants. Artificial silk should also be excepted. This is made from plant substances, but not necessarily from fibers. The flax plant produces in its bark very fine, tough fibers from which linen thread and fabrics are made. In countries about the Mediterranean, flax has been cultivated for thousands of years. The most important of fiber plants is cotton, a member of the mallow family to which also belong the hollyhocks. Cotton fibers are hairs that grow out from the epidermal cells of the seed coat. Cotton has been grown from very ancient times; at present more than half the world's supply is produced in the United States. In the phloem of the stem of hemp, a representative of the nettle family, is a mechanical tissue composed of tough fibers from which sail cloth, sacking, binder twine, carpet yarns, thread, rope, and oakum are made. Jute, belonging like basswood to the linden family, is the fiber plant that chiefly competes with hemp. Jute fiber is extensively used in the manufacture of sugar sacking, gunny sacks, burlap, and wool sacking. Although jute is easily cultivated in most warm climates, it is grown most extensively in India. Sisal, largely used for binder twine, is obtained from the leaves of an agave, a plant of the amaryllis family related to the lilies. This agave is grown principally in Yucatan. The plants mentioned are the leading sources of plant fibers, but the fibers of many other plants also are of practical importance.

Most of the coloring matters used as dye-stuffs were obtained

from plants until the manufacture of aniline dyes resulted in their displacement; some vegetable dyes, however, are still much used.

413. Crop-distribution. The climatic conditions that determine the geographic distribution of plants in nature affect also the distribution of crop plants. Each crop grows best in certain regions, and this fact largely determines the location of industries dependent upon special plants. The climatic conditions most commonly

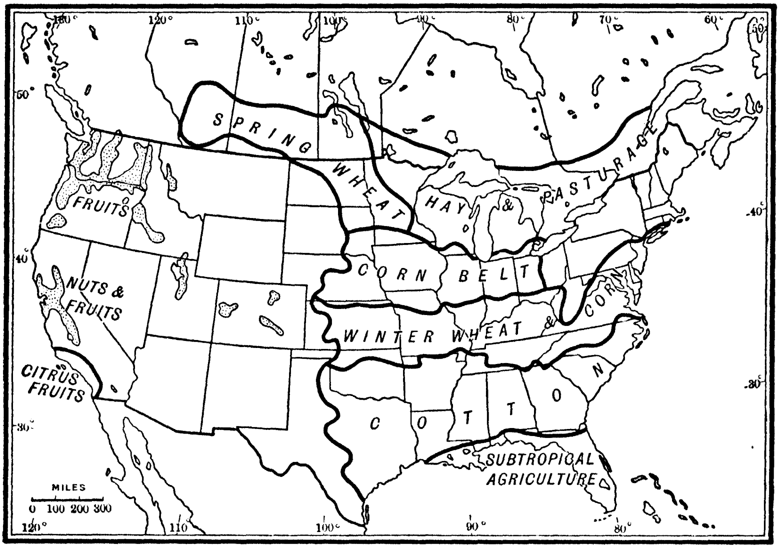


FIG. 414. Chief crop areas of the United States and Canada.

affecting the distribution of crops, as well as of most wild plants, are moisture, temperature, and light. A study of the natural vegetation of a region and of the conditions favorable for particular associations of wild plants often suggests the kind of crop best adapted to that region. Each crop plant has its own particular requirements, although the requirements of several species may be similar; climatic conditions largely determine, therefore, which crop or crops will be best suited to a given locality.

The physical and chemical nature of the soil affects crop-production favorably or unfavorably. Every soil differs to some extent from every other soil. Pure sandy soils contain almost no soluble materials; "alkali" soils are highly impregnated with soluble inorganic salts. In most ordinary soils the solutions present

contain about the same kinds and proportions of soluble substances, but such soils differ very greatly with respect to the insoluble organic matter present. It follows that within any climatic region there may be many different soil habitats, in each of which some crops will grow better than others.

The geographic distribution of important crop plants of the United States is found to correspond in general to the well-known

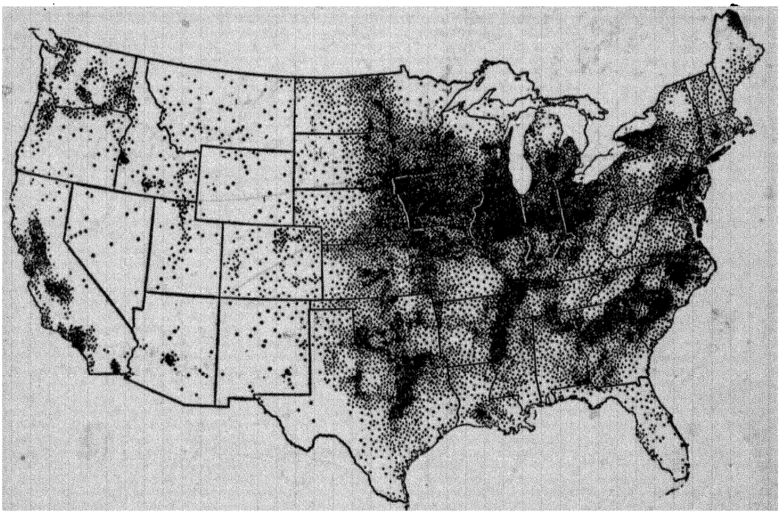


FIG. 415. Distribution of the agricultural lands of the United States on the basis of the value of their products. Each dot represents $1,000,000. From the Yearbook of the U. S. Department of Agriculture.

centers of natural vegetation. Timothy, spring wheat, rye, buckwheat, and potatoes occupy the same region as the northeastern forest trees; corn, winter wheat, oats, red clover, and beans are the crops that dominate the central region; cotton, tobacco, sweet potatoes, cowpeas, and peanuts predominate in the southeastern forest region.

In the New England states and New York, over half the cultivated land is devoted to the growing of hay and other forage crops, and much land is used for pasturage. The climatic conditions and the topography of this region render the production of cereals less profitable. Apples, grapes, and other fruits thrive, especially near Lakes Erie and Ontario.

Cotton is the principal crop of the southern states. Although

much cotton is shipped to New England and abroad for manufacture, much is manufactured in the South. The production of cottonseed oil is an industry of the southern states. In North Carolina and Tennessee, tobacco occupies the same region as cotton. Tobacco is largely grown also from Kentucky northeastward into Virginia. In the cotton regions of Louisiana, sugar cane and rice also are grown. Rice is grown in the same region as to-

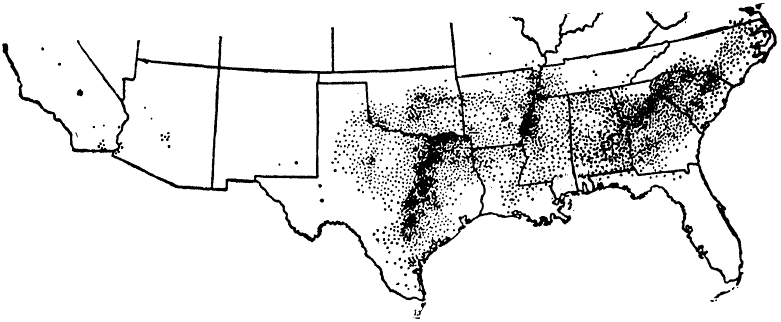


FIG. 416. Acreage planted to cotton in the United States. Each dot represents 10,000 acres. From the Yearbook of the U. S. Department of Agriculture.

bacco in Texas. Sweet potatoes, cowpeas, and peanuts are raised in most of the cotton belt.

The corn belt embraces the region from Ohio to eastern Kansas and Nebraska. This region produces more than half the corn crop of the country, eastern Illinois being the greatest productive center. The corn belt has a more fertile soil than any other region of similar extent, containing a larger proportion of humus, and has sunny summers, a relatively high summer temperature, and a comparatively heavy annual rainfall. The great cattle markets and packing industries are located in the corn belt, and various corn products are there manufactured. Other crops, such as wheat, oats, hay, and sweet corn, also are grown in the corn belt; but they are of secondary importance in this region. Sugar beets are raised in an area lying in general north and west of the corn belt, the centers of sugar-beet production being in Colorado and Michigan.

Extending from the Mississippi westward to the foothills of the Rocky Mountains, grasslands predominate. This region is characterized by pronounced climatic variations, especially with respect

to rainfall and evaporation. The natural vegetation of the eastern portion, the prairies, differs from that of the western portion, the plains. The true prairies extend roughly from North Dakota to Texas and eastward to Indiana. It is in these central prairies that, as already mentioned, the bulk of the corn crop of the United States is produced. The northern portion of the prairies is the leading region for the production of spring wheat, which centers

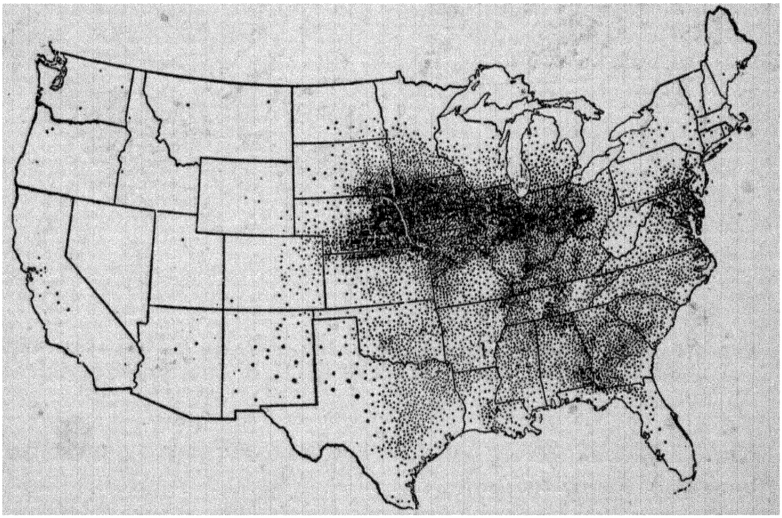


FIG. 417. Regions of the United States planted to corn. Each dot represents approximately 10,000 acres. From the Yearbook of the U. S. Department of Agriculture.

in North Dakota; the center of the production of winter wheat is in Kansas. Because of the presence of water power and of its nearness to the wheat-growing centers, Minneapolis is the leading flour-milling city of the world. Large quantities of flax and barley also are raised in the northern prairies.

Between the prairies and the foothills of the Rockies are the Great Plains, extending from Saskatchewan on the north to Texas on the south. The plains, which were originally the grazing lands of the buffalo and later were occupied by cattle ranges, possess a drier soil than that of the prairies. The introduction of plants that can conserve moisture or utilize the available water has made it possible to grow certain crops in this area, so that, in addition to grazing, some portions of the plains are used for farming pur-

poses, producing much alfalfa and such hardy wheats as durum. Farther south, especially in western Kansas, "Kafir corn" (a grain-producing sorghum) and millet (milo) are successfully grown. The production of broom corn, another variety of sorghum, centers in Kansas, Oklahoma, and Texas. Grazing, pasturage, and

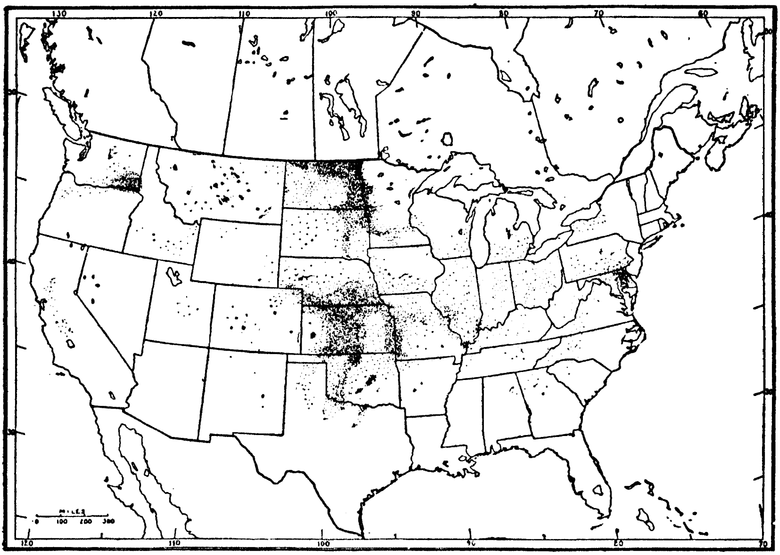


FIG. 418. Wheat-growing areas of the United States. Each dot represents approximately 25,000 acres.

the raising of forage crops are therefore the chief agricultural activities of the Great Plains.

The native flora of the states of Washington, Oregon, and California, because of the great variations in topography and climate, is extremely diverse. Even the valleys, coastal and intermountain, vary greatly in their native vegetation, and crops of wide diversity are produced, especially in the drier sections when water for irrigation is available. The crops comprise forage plants, cereal grains, and fruits of many kinds both subtropical and tropical. In fact, some part of this region can be found that is adapted to the growing of almost any crop. The western portions of Washington and Oregon have the greatest average annual rainfall of any section of the United States.

Eastward from the Cascades, in the northern half of this region,

the elevations are greater and in general the rainfall is less. Much of this portion of the territory is timbered to a greater or less extent, but considerable parts are devoted to grazing and grain-growing. In eastern Oregon and Washington wheat-growing is important. Some of the intermountain valleys, where water is available for irrigation, are given over to fruit-raising. Apples are produced in large quantities in the moister valleys of Washington, Oregon, and Idaho. Other fruits of various kinds, such as peaches, plums, apricots, and berries, also are raised. Many of these crops are grown on the highly fertile irrigated soils of this region.

In northern California much grain is grown, and there is considerable range land in the drier parts of Oregon and California. Farther south, walnuts, plums, apricots, peaches, and grapes are important products. Irrigation has made the fertile soil of southern California especially valuable for the production of citrus fruits.

Plants Used in Medicine

414. Early Interest in Plants. Since very remote times plants or plant parts have been used as medicines, either in the cure of disease or in the treatment of wounds. The earliest studies of plants appear to have been made with a view to discovering or recording their usefulness either as food or in medicine. The foundations of the sciences of botany and zoölogy were laid by Aristotle and Theophrastus, who lived in Greece in the fourth century B.C. Aristotle chiefly studied and wrote about animals; Theophrastus studied and described plants. The latter may be considered the first scientific botanist, since he attempted to investigate plant structure, growth, and distribution, and recorded the names of about 500 different kinds of plants. In the first century A.D., Dioscorides, a Greek physician and medical officer serving with Roman legions, wrote a "Medical Botany" in which he devoted a chapter to each plant, animal, or other product of nature useful in medicine. The chapters on plants contain brief comments on the habitat and general distribution of each plant considered, an account of its root, stem, leaf, flower, and fruit, and a description of medicinal effects, methods of preparation, and usage. For more than 1,000 years Dioscorides' volume was one of the chief sources of information in the training of physicians.

In the first century A.D. also lived a popular Roman author,

Pliny the Elder. His "Natural History" was widely read throughout the middle ages. This work consists of 37 "books," of which 16 deal with plants and their agricultural, horticultural, and medicinal uses. Pliny was a compiler of information from earlier writers rather than an original investigator.

After the time of Pliny came a long period in which no additions were made to the knowledge of plants. In the fifteenth and sixteenth centuries a number of medical men in European countries published elaborate volumes called *herbals*. These books contain extensive descriptions of plants and are often accurately illustrated, many of the drawings having been made from nature. In the seventeenth and eighteenth centuries botanical science as such came slowly into being.

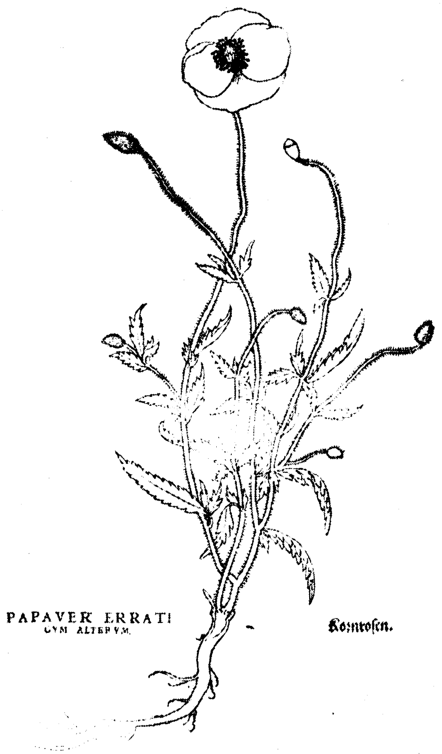


FIG. 419. Figure of a poppy from the herbal of Leonhard Fuchs, first published in 1542.

Botanical gardens were established at an early date. One of the earliest of these existed at Athens in the fourth century B.C. It was founded by Aristotle and after his death was carried on by Theophrastus. There is a record also of a garden of medicinal plants at Rome during the first century A.D.

415. Medicinal Plants and Drugs. In more modern times, at least until rather recently, the bulk of vegetable drugs has been obtained from wild plants; but this source has been in large measure exhausted, so that at present the cultivation of drug plants

is carried on to an ever-increasing extent. Of the plant drugs formerly in use, a number have been replaced or supplanted by synthetic chemical compounds, many of which are prepared from coal tar.

The substances contained in plant drugs which give them their medicinal properties are of varied nature; among these substances are alkaloids, glucosides, volatile oils, and oleoresins. The active constituents of a drug may occur throughout the entire plant or only in certain of its organs. Plant drugs are classed by pharmacists as herbs, barks, woods, leaves, roots, rhizomes (underground stems), bulbs, tubers, flowers, flowering tops, floral parts, seeds, and fruits.

A drug composed of the whole plant is called an "herb." Peppermint, spearmint, and lobelia are examples. The active constituent of an "herb" is often localized in certain parts of the plant; thus, peppermint and spearmint owe their medicinal properties to a volatile oil produced in glandular hairs which are found principally on the leaves and stems.

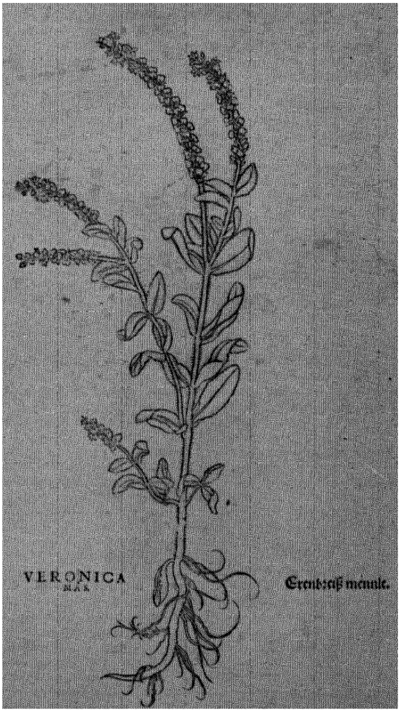


FIG. 420. Figure of Veronica from Fuchs' herbal.

One of the most valuable barks is that of the cinchona tree, found originally in Peru but now cultivated largely in the East Indies. From it is obtained the alkaloid quinine, a specific cure for malaria. The bark of *Rhamnus purshiana*, a tree growing in Oregon, Washington, and California, is known as "cascara"; it supplies a valuable cathartic. From *Quillaja saponaria*, a tree of Peru and Chili, soapbark is obtained. Its

principal constituent, saponin, is a mixture of glucosides. Saponin is used to some extent in medicine, but its greater use is as a foam-producer in beverages.

One of the woods most used in medicine is sandalwood, coming from India and the East Indies. It contains a volatile oil, used as a perfume, and medicinally in diseases of the mucous membranes. Camphor is obtained by passing steam through the finely chipped wood and bark of a tree growing in Formosa, China, and Japan. It is used because of its stimulative properties. Oil of turpentine and rosin are derived from the wood of the long-leaf pine and other pines. Tar is obtained by the destructive distillation of pine wood.

The leaves of the coca plant, grown in the mountains of Peru and Bolivia, contain cocaine, used as a local anesthetic in minor surgery. Cocaine is one of the most widely used habit-forming drugs. Other leaves much used in medicine are those of belladonna, digitalis, senna, and henbane.

Among root drugs, ipecac from Brazil and Bolivia is one of the most important. It is used as an emetic and in cough mixtures. The dandelion and burdock are common weeds whose roots have medicinal qualities. Licorice is known to every child. Its use in medicine is principally to modify the taste of bitter drugs.

Of the rhizomes, ginger is used both as a condiment and as a medicine. Golden seal, formerly abundant in the northern United States, has been in such demand on account of its tonic properties that it has almost disappeared from that region and is now being cultivated to some extent. The rhizome of valerian is a nerve stimulant. The rhizomes of wild geranium, bloodroot, and may apple are used as drugs. In the case of rhubarb, both rhizome and root are used. The medicinally valuable rhubarb comes from western China and Tibet.

Camomile, arnica, and santonica are drugs prepared from the flowers of members of the composite family. Cloves are dried flower buds and are useful because of their high percentage of a volatile oil.

The part of the Indian hemp used in medicine is the whole flowering top of the pistillate plant. The important constituent is a resin, cannabin. Hemp is sold in the bazaars of India for smoking purposes under the name of "gunjah." When mixed with aromatic drugs it is called "hashish." It is a powerful narcotic. Most of the poisons of plant origin, like cannabin, are useful as drugs in

small doses. Strychnine and brucine are alkaloids obtained from the seeds of *Strychnos nux-vomica*, a small tree growing in India and the Philippines. These alkaloids are stimulants and nerve tonics. The Calabar bean or ordeal bean from western Africa is another drug plant whose seeds contain poisonous alkaloids. Its action is opposite to that of strychnine, and it is used as an antidote in cases of strychnine poisoning. The kernel of the seed of the bitter almond contains hydrocyanic acid (prussic acid) and is used in medicine as a sedative.

Many fruits of members of the parsley family contain volatile oils used in medicine. Anise, fennel, caraway, and coriander are familiar examples. Vanilla "beans" are the long, slender fruits of a Mexican epiphytic orchid.

In addition to the drugs already mentioned, which consist of whole plant organs, there are many medicinal substances composed of cell contents or of secretions. Opium is the thickened latex from the fruit coat of the poppy. It contains, besides morphine and codeine, a number of other alkaloids. The drug known as aloes is prepared by condensing the mucilaginous juice obtained from the fleshy leaves of a number of species of Aloe, a subtropical genus of the lily family. Gum arabic is an exudation from the wounded bark of *Acacia senegal* and other species of Acacia. Myrrh is a gummy resin obtained from a shrub growing in northeastern Africa. It is used in incense as well as in medicine.

Large quantities of volatile oils derived from plants are used in the manufacture of perfumes. These oils are mostly imported from England, Germany, France, and Mediterranean countries. Some of the best-known oils so used are those of rose, lavender, rosemary, rose geranium, bergamot and other citrus fruits, sandalwood, and bay.

Forestry and Forest Products

416. Forest Reserves. The early settlers in America used land mainly for hunting and pasturage; later, when agriculture became an important pursuit, it was assumed that timber was so abundant as to be inexhaustible, and forests were destroyed with no serious thought for the future. A similar reckless destruction of forests had taken place in Europe long before; but as early as the tenth century, laws were adopted by many German, Swiss, and French cities and states, controlling the cutting of timber and providing

for the planting of new forests. In consequence, forest areas have been established under government control in some European countries, assuring a continuous supply of timber.

Although sporadic efforts had been made at different times in the United States, both by the states and by the national government, to protect the timber supply, it was not until 1876 that definite plans were formulated on a national scale. In 1891 Congress authorized the President to set aside as forest reserves lands wholly

FIG. 421. Pine seedlings in a forest nursery containing 5,100,000 trees. From the bare plots at the left 1,065,000 trees have been removed for transplanting. Photograph from the New York Conservation Commission.

or in part covered with timber. During the Harrison administration reserves totaling more than 13,000,000 acres were established; during the Cleveland administration 22,000,000 acres were added. President McKinley established a few forest reserves; in the succeeding Roosevelt administration more than 150,000,000 acres were reserved and a thorough-going forestry policy was established. Much land has since been added; some has been released or sold. There are now in the national forest reserves, including Alaska and Puerto Rico, approximately 200,000,000 acres. Many states have established forest reserves, and each year these reserves are being increased and so supervised that they will continue to furnish timber for future generations.

417. Lumbering. Because the supply seemed inexhaustible, only the largest trees were selected and only the better portions of felled trees were saved. The other portions left on the ground became dry, and in these "slashings" serious forest fires often started which destroyed much of the timber still standing. Sawmills, too, used only the better portions of a log, and it is estimated that not more than one fourth of a selected tree was finally made into lumber. The extensive forests of white and Norway pine which

FIG. 422. Cut- and burned-over forest lands in Minnesota. Photograph by the U. S. Forest Service.

covered great areas in the northern and eastern states were almost destroyed by these methods. Much southern yellow pine and large stands of hard woods throughout the country also have been destroyed.

At present lumbermen are using larger portions of the trees that are cut, the slashings are so handled as to minimize the fire risk, and sawmills are using much of the former waste material in the manufacture of by-products. Forest rangers, supported by the national government, states, and individual timber owners, are doing much to check forest losses. A policy of replanting cut-over areas is each year adding thousands of acres to the available timber supply.

418. Utilization of Forest Products. Although the greater part of the timber cut is manufactured into lumber, much is used for other purposes. Among articles made from timber are firewood, telegraph poles, railway ties, fence posts, mine timbers, barrels, and pails. Much material of the sort once wasted is made into spools, toys, and matches. Firs and spruces, which still form extensive forests in the northern United States and Canada, furnish

FIG. 423. A cultivated forest of Norway spruce in Europe. Photograph by the U. S. Forest Service.

pulpwood for the manufacture of paper; other woods, both soft and hard, also are now utilized for this purpose.

Oak and hemlock bark and the wood of the chestnut are the favorite materials for use in the tanning of leather. But since the supply is limited, various other barks and woods as well as chemical tanning agents are likewise used.

Resin is an exudate secured from certain species of pine in the southern states, long-leaf pine furnishing the greater part of the supply. Distillation of resin yields turpentine ("oil of turpentine"); the solid portion remaining is rosin. Turpentine is obtained also by dry distillation from the waste materials of sawmills, including slabs and sawdust. This latter process of distillation yields various other products, including tar, pyroligneous acid, crude oils, and charcoal. Charcoal is made also from various hard

woods; additional substances obtained in its production are acetate of lime, acetone, and tar. Large quantities of sawdust and shavings are ground, chemically treated, and molded under pressure to make many articles formerly made of hard rubber.

Veneers (thin slices) were formerly produced only from the more expensive woods; but the demand is now so great that the making of veneers has become an important industry. Red gum, yellow pine, maple, yellow poplar, cottonwood, white oak, and birch are among the many timbers used in the manufacture of veneers for doors, furniture, and partitions. The slices average about 1/40 inch in thickness. It is estimated that almost a half billion feet of wood are used each year in this industry. Basswood, cottonwood, yellow pine, and yellow poplar are made into excelsior, used for upholstering, packing, and various filtering purposes.

The sap of the hard maple is obtained by boring holes into the trunk near its base. "Tapping" is done during late March and early April, and the sap is boiled down to make maple syrup or maple sugar. The maple syrup industry is confined chiefly to New Hampshire, Vermont, northern New York, and some of the states bordering the Great Lakes.

Weeds

419. What Is a Weed? The term *weed* is applied to any plant that is growing where it is not desired. Most ordinary weeds are seed plants, although some ferns and horsetails are so considered. Some weeds belong to species that are or have been cultivated, but that become troublesome when they interfere with the growth of useful crops of other plants. Horse-radish and Johnson grass are examples of cultivated plants which have become injurious weeds in certain localities. Some plants are innocuous in their native habitats but become nuisances when they invade a new locality. In general, most of the aggressive weeds have been introduced from other countries; but some native plants under special circumstances may become weeds. Although in almost every locality many species of plants grow wild and many appear among crops, comparatively few are objectionable weeds.

420. Dissemination. In order to compete with farm and garden plants, weeds must be able to survive unfavorable influences and to increase their numbers with great rapidity. Very commonly, weeds are distinguished by a marked power of vegetative mul-

tiplication. Many possess deeply growing, tough, or extensive root systems; others have widespreading underground stems and branches which in some cases give rise to many aërial shoots. If the underground parts are cut into pieces by farm implements, each piece may produce a new plant. The Canada thistle, for example, has a branching underground stem, the branches of which become separate plants by the destruction or death of the older parts. Some grasses which are weeds are multiplied in a similar manner. Certain plants, such as some of the hawkweeds, produce runners above the ground which, when separated, give rise to new plants. Other weeds, like nut grass, multiply by means of tubers.

Most weeds are spread also by means of seeds which may be sown with the seeds of crop plants. Such weeds are introduced into fields together with grass, clover, or other commercial crops. Weeds are often unavoidably harvested with crop plants, and their seeds are then distributed with those of the crop; chess seed, for example, is distributed with wheat, wild oats with cultivated oats, and dodder with clover and alfalfa seed. Weed seeds are spread also by threshing machines and other farm implements, as well as by railway trains and automobiles, so gaining a foothold along railway tracks and highways and spreading thence to neighboring farm lands. Seeds are frequently spread also in stable manure and in other litter of farmyards and stables.

421. Weeds of Various Regions. Regions differing in soil and climate differ also with respect to their prominent weeds. A particular weed may be troublesome in one part of the country and not in another. Quack-grass, an annoying weed from Maine to Minnesota, is not so serious a pest in the southern states; on the other hand, Johnson grass, practically unknown in the North, has escaped from cultivation and become a weed in the South. Soil moisture is an important factor in determining the distribution of weeds. Cacti are weeds from central Kansas westward and southward, but do not grow to any extent farther east and north. Some verbenas, the common mullein, and everlastings occur as weeds in dry pastures. Certain ferns, smartweeds, mints, and dock grow only in meadows and moist pastures. With the removal of forests, many weeds introduced from Europe found a favorable environment in the soil once occupied by less hardy native species and spread rapidly as cultivation increased. As the area of cul-

tivation extended westward beyond the forested regions, some native species of the prairies, such as cocklebur, verbena, and horse nettle, contributed to the weed flora. Once the black-eyed Susan grew only west of the Alleghenies, but it is now an abundant weed throughout the eastern states.

422. Injuries Caused by Weeds. Weeds are harmful in various ways:

(*a*) They absorb from the soil moisture and salts required by useful plants.

(*b*) They crowd out useful plants because, as a rule, of their numbers and their rapid growth. Rapidly growing weeds also shade shorter plants and seedlings, so interfering with photosynthesis.

(*c*) Some weeds, like the dodders, are parasitic on useful plants and rob them of their foods.

(*d*) Some parasitic fungi, like the rusts, pass a part of their life upon weeds which thus provide an opportunity for the overwintering of the fungi. Other weeds furnish food for insects injurious to useful plants. The potato beetle lives on many plants of the nightshade family, from which it migrates to potato plants. Stubble with which weeds are intermingled furnishes places for cutworms.

(*e*) Some weeds are poisonous, injuring domestic animals; such weeds are lambkill (sheep laurel) and water hemlock. Hemp and the "loco weeds" produce symptoms of intoxication and poisoning in horses and sheep. Many plants also contain poisonous substances injurious to man.

(*f*) The seeds and fruits of some weeds cling to domestic animals. Burs on sheep render their wool less useful. Some spiny plants injure stock; for example, thorny shrubs are a great source of trouble to wool-growers. The horny and barbed fruits of some grasses irritate or wound the mouths of grazing animals.

(*g*) Certain weeds, such as wild garlic and stinkweed, when eaten by cows, taint their milk and render it unfit for human consumption.

(*h*) Weed seeds diminish the commercial value of crop seeds with which they are mixed.

423. Control. In order to control or exterminate weeds, a knowledge of their habits and reproductive methods is necessary. Annual weeds may be eradicated by any method that will hasten the germination of their seeds and then destroy the young plants.

Biennial weeds should be cut down or plowed under before they have an opportunity to produce seeds in their second year. Perennial weeds are most troublesome and most difficult to destroy. Cutting down the plants, plowing them under, and destroying their underground parts are methods employed for their eradication. Seeds used for crops should be as free as possible from weed seeds, and care should be taken not to spread weed seeds in stable manure. All places favorable for the growth of weeds should be cultivated, or the weeds should be otherwise removed.

Plant Diseases

424. Nature. When, as a result of external conditions, the ordinary or "normal" functions of a plant or of its parts are inter-

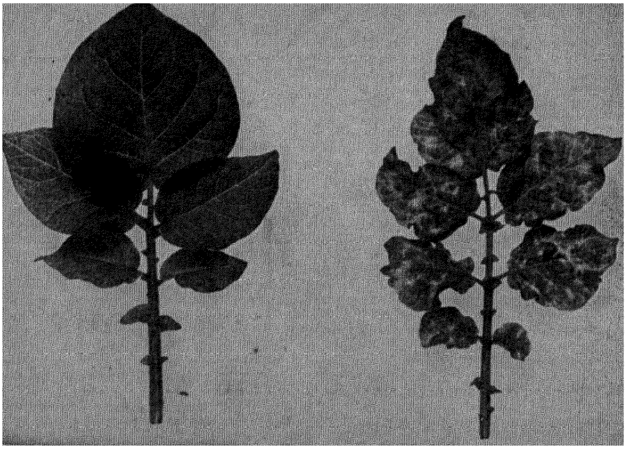


Fig. 424. Mosaic disease of potato. At the left an uninfected leaf; at the right an infected leaf. Photograph from James Johnson.

fered with or deranged, the plant is said to be *diseased.* The various ways in which the structure and functions of the plant are thus caused to deviate from the normal condition are spoken of as *symptoms.* A very large proportion of plant, as well as of animal, diseases result from the attacks of other organisms. In such a case it is the parasitic organism that causes the disease and not infrequently the death of the host.

Many parasitic animals are capable of entering and living in the tissues of plants; among the most common of these are species

of nematodes or "eel worms." Nematodes are often root parasites, their presence in roots resulting in the formation of galls. The wheat nematode and some others of the group can invade all portions of the host plant and entirely check the formation of normal fruits.

Among parasitic plants are some that contain chlorophyll. Certain algae, for example, live in the tissues of more complex plants, sometimes doing no injury to the host but at other times causing disease. Of parasitic seed plants the best known are the mistletoes and dodders.

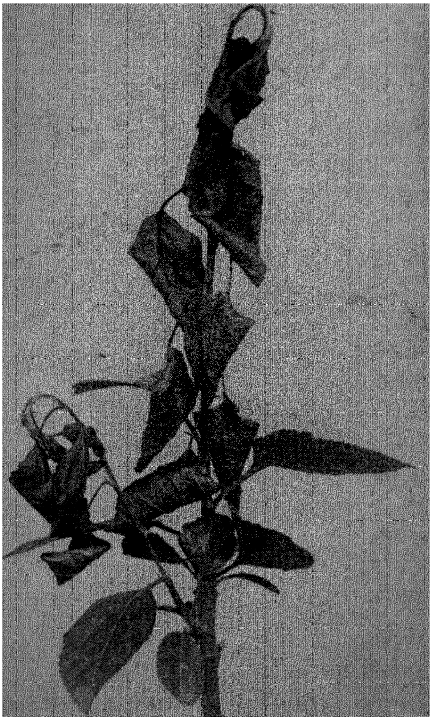


FIG. 425. Fire blight of pear.

425. Virus Diseases. There are a considerable number of plant diseases for which, as for such human diseases as scarlet fever and cancer, no causal organism has been found. Among the more common of these are the "virus" or mosaic diseases of potato (Fig. 424), tobacco, and cucumber. Each of these hosts may be attacked by several virus diseases. The mosaics of these and of some other plants can readily be transmitted from plant to plant. The mosaic diseases of the peach, including "yellows," are transmitted under natural conditions in a manner not yet understood. Artificially, peach yellows can be transmitted only by means of grafting or budding. Some virus diseases, like aster yellows and "curly top" of the sugar beet, are transferred only by specific insects. As in the case of certain animal viruses, the active agent of such a plant disease must have spent some time in the body of

the insect carrier. The virus diseases of some members of the pulse family differ from most of this class in that they may be transmitted through seeds.

The symptoms of virus diseases are variable; in most cases the leaves of the host are malformed, stunted, and wrinkled; often they are mottled in appearance. In a few cases the entire plant is badly stunted; in others the number of leaves is greatly increased but they are abnormal in size and color.

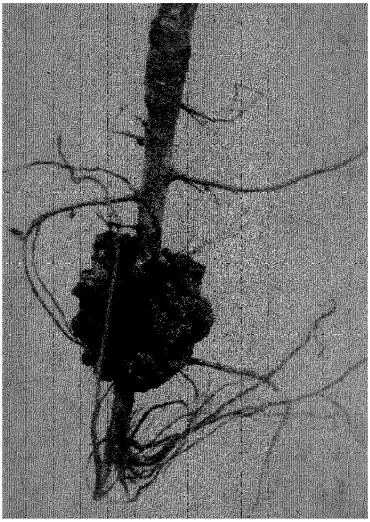


FIG. 426. Crown gall of apple.

426. Diseases Caused by Bacteria. One of the commonest bacterial plant diseases is the "fire blight" or "pear blight" (Fig. 425), which occurs on the apple, crab apple, pear, and related plants. The bacterium causing this disease gains entrance to the host through wounds, or more often through the floral nectaries, and multiplies very rapidly, killing the host cells so quickly that the affected portion appears scorched. At the end of the growing season, the bacteria remain dormant at the edges of the diseased portion; when the host plant resumes growth the following spring, the bacteria again multiply rapidly and are often exuded in a viscous liquid. Insects visit this exudate and carry the bacteria to other plants.

"Soft rot," caused by bacteria that enter the host through wounds, is responsible for the rotting of many vegetables in the field, and for still further losses if the diseased vegetables are stored in warm, moist places.

Cabbage is attacked by a black rot caused by bacteria that enter the leaves of the host, usually through water pores. The bacteria travel through the conducting elements of the xylem, multiplying so greatly as to clog these elements. The water supply is thus cut off from the tissues of the plant, and if the main stem is invaded the whole plant may die.

"Crown gall," so called because of the large galls formed on stems and roots at the surface of the soil, is a serious disease of apples (Fig. 426), and is abundant also on many other plants, including raspberries, grapes, and walnuts. The bacteria enter through wounds; the stimulus supplied by their presence causes a rapid division of the host cells in their vicinity, as well as a marked enlargement of many of these cells.

427. Diseases Caused by Slime Molds. Slime molds have certain characteristics possessed by fungi and others common to some very simple animals. When studied by botanists, slime molds are included among the lower fungi.

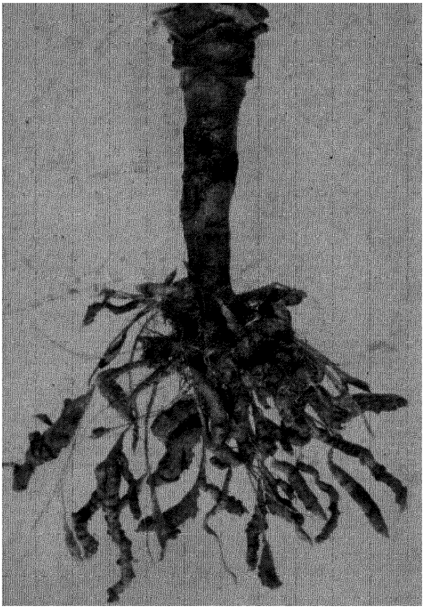


FIG. 427. Clubroot of cabbage. The swellings of the roots are caused by a parasitic slime mold (Plasmodiophora).

The plant body of a slime mold is a naked mass of protoplasm (*plasmodium*) containing when fully developed very many nuclei. Most slime molds are saprophytic, but a few are parasitic in the tissues of higher plants. The saprophytic forms when mature develop fruiting bodies (sporangia) of various sizes and shapes, within which by cell division one-nucleate spores are formed.

The strictly parasitic slime molds do not produce fruiting bodies. A plasmodium of one of these species divides within the host tissue into masses of spores, which masses may be irregular or may take on a characteristic form. One of the best known of these parasitic slime molds (Plasmodiophora) causes a disease (clubroot) of cabbage and related plants (Fig. 427). The parasite enters a root of the host plant in the form either of an amoeboid cell or of a very small plasmodium, which enlarges in a cortical cell of the root.

As a result of the stimulus due to the presence of the fungus, the host cell grows and divides. The division of the host cell is often accompanied by a division of the plasmodium within it. In consequence of the repeated growth and division of the original host cell and of its offspring, large swellings appear on the roots of the host plant. Most of the cells of these swellings contain plasmodia. The plasmodia grow, consuming the contents of the host cells, until they fill or almost fill the spaces within the cell walls of the host. Finally, the plasmodia divide into one-nucleate spores which are liberated when the host tissue breaks down.

Closely related to Plasmodiophora is an organism causing the "powdery scab" of potatoes. This disease has long been known in Europe, and in some localities is very destructive. It appeared in the extensive potato-growing areas of southeastern Canada and adjacent parts of the United States about 1910; here it has been practically eliminated by the sterilization of tubers before they are planted, and by the growing of resistant varieties. The slime mold causes the formation of blister-like spots on developing tubers; the spots increase greatly in size and become filled with a brownish powdery substance composed of broken-down host tissues together with the spores of the fungus.

428. Diseases Caused by Phycomycetes. The serious diseases due to Albugo, Pythium, Plasmopara, and Phytophthora were mentioned in Chapter XIX. The damage done by the "downy mildew" of the grape (Plasmopara) and the "late blight" of potato (Phytophthora) has been greatly checked in the United States by systematic spraying of the host plants. Another phycomycete (a chytrid, Urophlyctis) attacks alfalfa in the irrigated regions of the West. The fungus invades the young alfalfa buds at the surface of the soil, checks their development, and causes the formation of numerous galls. Aphanomyces, related to Saprolegnia, attacks the roots of many leguminous plants and sometimes causes serious losses through the breaking down of the tissues of the roots, so preventing the transportation of water.

429. Diseases Caused by Ascomycetes. Besides the powdery mildew of the lilac (§ 219), a number of powdery mildews cause plant diseases some of which result in considerable damage.

One of the simpler ascomycetes (Taphrina) causes "plum pocket." The younger branches, leaves, and fruits of the plum, invaded by this fungus, are stimulated to excessive growth. The

fruit often becomes hollow, the pit being absent. After a period of rapid vegetative growth, the fungal hyphae grow to the outside of the part affected and on its surface form many asci. Peach, poplar, alder, hazel, and other hosts are attacked by various species of Taphrina.

The apple and pear are often injured by species of Venturia, which produce a dark-colored mycelial growth on the leaves and fruits. The mycelium penetrates only the cuticle, but the growth of the epidermal and immediately underlying cells of the host is checked. Infected fruits are often very irregular in shape and sometimes display large cracks. Conidia, formed at the ends of protruding hyphae, spread the disease during the growing season. After the leaves fall, the fungus penetrates them and continues to grow as a saprophyte. In the dead leaves, small rounded fruiting bodies containing asci are developed which mature the next spring and liberate ascospores that can infect new hosts.

FIG. 428. Brown rot of plum.

Cherries, plums, and related plants are attacked by species of Sclerotinia (Fig. 428); infected fruits decay and turn dark brown. Many conidia are produced by the aërial hyphae on the surfaces of the decaying fruits, and if there is ample moisture the disease is spread by the conidia from tree to tree. This "brown-rot" fungus remains alive in fruits that fall to the ground and in the following spring renews its growth, forming saucer-shaped fruiting bodies containing many asci. The ascospores, liberated during spring rains, communicate the disease to the newly forming fruits.

About 1910, a disease was discovered on chestnut trees in the vicinity of New York City; during succeeding years it spread throughout the chestnut forests of New York and neighboring states. So serious was the disease and so rapid its spread that all

efforts made by state and national governments failed to check it, and the chestnut forests in the northeastern United States have been almost entirely destroyed. The disease is caused by an ascomycete, probably introduced from Japan where it has long been known but does little damage.

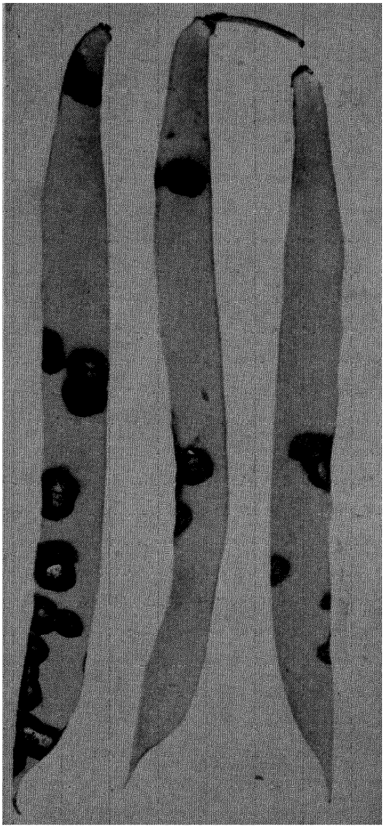


FIG. 429. Anthracnose of bean.

430. Diseases Caused by Basidiomycetes. All cereal grains and many wild grasses are attacked by one or another of the smuts (Chap. XXI). Serious diseases of the onion, of rice, and of many leguminous plants also are caused by smuts.

In addition to those discussed in Chapter XXI, various species of rusts are parasitic upon the great majority of seed plants, both cultivated and wild. Some attack ferns as well. The "blister rust," which threatens the existence of white pines in the United States and Canada, was imported from Europe on pine seedlings. The stage of this rust that produces uredo- and teleutospores is passed on currants and gooseberries. One means being used in the attempt to control the disease is the extermination of cultivated and wild currants and gooseberries in the neighborhood of white pine forests.

431. Diseases Caused by Imperfect Fungi. Imperfect fungi are so called because they or many of them are thought to be ascomycetes or basidiomycetes whose life cycles are only partly known. The part of the cycle which is known in each case produces spores of varied types, but does not include the ascospore- or basidiospore-forming stage. Each year the study of these fungi reveals

the unknown stages in the life cycles of some of them, which are then transferred to the appropriate class (ascomycetes or basidiomycetes). Many thousands of species of imperfect fungi are known, a large proportion of them being parasitic and causing diseases of bryophytes, pteridophytes, and especially of seed plants. Among the diseases that they produce are the early blight of potato, the leaf spot of beets, anthracnose of beans (Fig. 429), and cabbage yellows.

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